

Reports
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E. D.

FINAL REPORT:MIPR 92-248

PROPAGATION AND BIOLOGY OF CRYPTOBIOTIC CRUSTS

December 31, 1992

**E. Durant McArthur
USDA Forest Service
Intermountain Research Station
Shrub Sciences Laboratory
Provo, UT 84606**

**To: US Army Corps of Engineers
Construction Engineering Research Laboratory
Champaign, IL 61826-9005**

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324 25th Street
Ogden, UT 84401

Reply to: 1530

Date: JAN 12 1993

Dr. Steve Warren
U.S. Army Corps of Engineers
Construction Engineering Research Laboratory
P.O. Box 9005
Champaign, IL 61826-9005

Dear Dr. Warren:

The final report for the Interagency Agreement, Propagation and Biology of Cryptobiotic Crusts, MIPR 92-248 is enclosed. The report consists of four separate documents bound together: 1) Military Base Cryptogamic Crust and Vegetation Analysis by Kimball T. Harper (INT-89412-GR); 2) Military Base Cryptogamic Crust and Vegetation Analysis: Water Erosion Analysis by James P. Dobrowolski (INT-91623-GR); 3) Cryptobiotic Crust Biology and Management in Arches and Canyonlands National Park by Jayne Belnap (INT-92686-JA, Interim Report); and 4) Propagation of Cryptogams for Use in Land Stabilization by Larry L. St. Clair (INT-92741-GR, Study Plan).

Competition of items 3 and 4 above are pending. We understand that work may be supplemented by a new MIPR. In any case, final reports will be submitted when those activities are completed. Please refer any questions to Dr. E. Durant McArthur of our Shrub Sciences Laboratory, 735 North 500 East, Provo, UT 84606, (801) 377-5717.

It has been a pleasure to cooperate with you and your agency. We look forward to continued work.

Sincerely,

181 Carlos L. Elwood

CARLOS L. ELWOOD
Budget Officer

Enclosure

cc: McArthur, SSL



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BRIGHAM YOUNG
UNIVERSITY

8 December 1992

Dr. E. Durant McArthur, Project Leader
Shrub Sciences Laboratory, Intermountain
Research Station
U.S. Forest Service
735 North 500 East
Provo, Utah 84606

Dear Durant:

I have enclosed an annual report on our work on the Army Corps of Engineers contract at Dugway Proving Grounds, Tooele Co., Utah. The report is in four parts: 1) results of water infiltration trials on the Dugway plots, 2) results of collaborative work with Dr. Rosemary Pendleton on the effects of cryptobiotic crusts on colonization of associated vascular plant roots by vesicular, arbuscular mycorrhizae, 3) the influence of various mechanical disturbances to cryptobiotic crusts on nitrogen fixation in those crusts at Dugway, and 4) a manuscript by Jaynie Belnap and I on the influence of cyanobacterial rich cryptobiotic crusts on uptake of essential mineral elements by two associated seed plants. I will briefly discuss each of the attached reports here.

1. The infiltration studies show that soils that were wet when the howitzer travelled over them had slower infiltration rates in both 1991 and in 1992 than did intermixed plots that were dry at the time of treatment (Table 1). The effect was nearly gone by August 1992 when the infiltration trials were run. It is significant that prewetted soils displayed significantly greater increases in infiltration rates in 1992 relative to 1991 than did dry plots. That differences if probably related to shrinkage and crack formation in the clay loam soils at the test plots. Since the prewetted soils had probably not dried to a water content equivalent of that of unwetted soils by August of 1991, fewer deep cracks and slower infiltration would be expected in those soils. By August of 1992 both soils had received far less precipitation than is normal for the site during the preceding 12 months. Consequently both prewetted and dry plots were extremely dry and had formed a conspicuous network of deep cracks interconnected in a polygon pattern, with polygons having an average diameter of 12-15 cm.

Scalped plots showed reduced infiltration rates relative to control plots (Table 2). The effect was particularly severe for plots that were both scalped and prewetted prior to trafficking with a tracked howitzer. That result may be related to the fact that during the scalping process, natural crack in the soil inescapably filled with soil fragments. The wetting treatment prior to trafficking by the howitzer probably washed those fragments farther downward and left them pliable enough to be pressed into durable plugs by the vehicular traffic. Even one year after treatment, the scalped and prewetted plots had an average infiltration rate that was only half that of control plots.

Plots crossed 10 times by the howitzer had an average infiltration rate that was between 25 and 30% that of control plots in both 1991 and 1992 (Table 3). A single pass of the howitzer reduced infiltration rates approximately 38% in 1991 (one month after treatment) and by about 42% in 1992 (13 months after treatment). Four passes reduced infiltration rate about 56% one month after treatment and about 42% 12 months later. All treatments

(including the control) showed greater infiltration rates in 1992 than in 1991. As expected, trafficked plots showed larger relative increases in infiltration rates than control plots (average of 56% increases versus 42% increase for control plots). These data suggest that a large part of the increased infiltration rates observed in 1992 is attributable to something other than natural recovery from the effects of traffic. As noted earlier, the 1992 water year was unusually dry and soils may have developed more cracks than existed in 1991. The year 1991 had natural precipitation supplemented by 5.0 cm of water applied per unit surface area to the prewetted plots which account for about half of the plots considered in Table 3. Wetting and drying and freezing and thawing processes would also cause swelling and shrinkage in the layer compacted by the howitzer traffic. Such processes would be expected to eventually restore normal bulk density and infiltration rates to compacted soils, but those processes can probably not account for more than a small portion (perhaps no more than 25%) of the observed increases in infiltration rates between 1991 and 1992 on trafficked plots.

2. Table 4 summarizes the mycorrhizal work with Dr. Pendleton. Those results show that not all vascular plant species roots are colonized by beneficial microbes: four annual species showed no mycorrhizal growth at all (two species in Boraginaceae and one species each in the families Loasaceae and Brassicaceae). Three other annuals (two grasses and a species in the family Plantaginaceae) did show some mycorrhizal development. For those species, there was always slightly more of the root length colonized when the plants grew on undisturbed, cryptobiotic crusts. One annual Lupine (a member of the Fabaceae) did not show mycorrhizal colonies, but its roots were heavily infected by nodule forming bacteria of the genus Rhizobium, a symbiotic nitrogen fixer. The infection was about 50% better developed in plants taken from a soil with a heavy cryptobiotic crust. The roots of the perennial grass, Stipa hymenoides, likewise were not colonized by vesicular arbuscular mycorrhizal, but they did often display well developed rhizosheaths. Rhizosheaths are modified rootlets that have developed prolific growths of root hairs and are heavily colonized in the decaying cortex region by the nitrogen-fixing, heterotrophic bacterium, Bacillus subtilis. Only 40% of the plants sampled on noncrusted soils developed rhizosheaths and all those plants showed only weak development of the rhizosheath. Plants from areas with well-developed cryptobiotic crusts all had rhizosheaths and on 60% of those plants, rhizosheaths were strongly developed.

The only shrubby species investigated was Coleogyne ramosissima, a long-lived shrub of the Rosaceae family. This species appears most commonly on shallow, sandy soils overlying creviced sandstone. Thousands of seedlings of this species appeared in southeastern Utah (Grand Co.) this year. Rosemary examined roots of 10 seedlings from soils without a cryptobiotic crust and 10 seedlings from soils with a heavy, cyanobacterial rich crust. On average, 5% of the root length of seedlings from disturbed areas without cryptobiotic crusts were invaded by VA mycorrhizal, but seedling roots from well crusted, undisturbed sites (within a stone's throw of the sites just discussed) showed VA infections along 18% of their root lengths.

3. The manuscript by Belnap, Harper and Warren reports on the effects of various forms of disturbance to the heavy, cyanobacterial-rich, soil-surface crusts at Dugway on nitrogen fixation and chlorophyll in the soil surface. The results demonstrate that all treatments [(1) shallow raking (breaks the surface cm of soil but removes nothing), 2) deep raking (a palaski is driven 1.0 dm into the soil at intersections of a 1.0 dm grid and the soil is pried up to break connections to the subsoil, but the soil blocks are not turned over), 3)

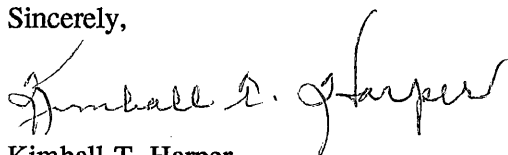
one pass of a 50 ton, track-driven howitzer, 4) 4 passes, 5) 10 passes of the howitzer, 6) scalped (surface 1.0 cm of soil with associated cryptophytes removed), and 7) scalped plus 4 howitzer passes] significantly reduced N-fixation relative to control plots. Average reduction of N-fixation for all treatments was 89%! Surprisingly, shallow raking which left all tissue in place reduced the N-fixation process as much as 10 passes of the howitzer which buried all of the cryptobiotic fragments. This may mean that the cyanobacteria involved are severely damaged (so far as nitrogen-fixation is concerned) by any mechanical disruption of the dry gelatinous sheaths that enclose cyanobacterial filaments in the dry season. That hypothesis is supported by the fact that the deep raking treatment had the greatest N-fixing capabilities of any treatment considered. That treatment greatly disturbed the soil (it was designed to break up the vesicular horizon which often occurred at 7-9 cm depth in the clay loam soil used for the experiments), but the cryptobiotic crust atop each 1.0 dm square disturbance block remained largely intact in the treatment. However, even the deep raked treatment showed less than 25% as much N-fixation as control plots.

Chlorophyll in soil was significantly reduced by scalping treatments and some of the heavier traffic treatments, but chlorophyll content of shallow raked, deep raked and single howitzer pass treatments was not significantly reduced relative to controls. Chlorophyll degradation to phaeophytin was unaffected by all treatments.

4. The enclosed manuscript by Belnap and I considers essential mineral uptake by Festuca octoflora and Mentzelia multiflora when grown in soils with well-developed cyanobacterial rich surface layers or in adjacent soil where foot traffic had eliminated the crusts. Plants on the crusted sites took up significantly more of certain essential elements. Festuca plants from crusted sites contained significantly more N, P, K, Ca, Mg, and Fe than plants grown on uncrusted soils a few meters away. Mentzelia plants from crusted sites contained significantly more N, Mg, and Fe than plants from nearby soils that were of the same origin and were similar in all respects except for the presence of the cyanobacterial rich cryptobiotic crust growth.

If you have questions about any of the foregoing, please call me at 378-2129.

Sincerely,



Kimball T. Harper
Professor of Botany

Table 1. The influence of prewetting prior to heavy equipment traffic on infiltration of water into soil through a single-ring, constant-water-head infiltrometer at Dugway Proving Grounds, August 1992. Plots were wetted with the equivalent of 5.0 cm of water per unit area one day before plots were traffic by a 50 metric ton, track propelled howitzer in July 1991. Plots were initially evaluated for infiltration rate in August 1991, one month after treatment. There were 21 replications per treatment per year.

Year of observation	Infiltration Rate (ml/5 min)		Significance of between Treatment Differences
	Treatment		
	Prewetted	Dry	
1991	22.2	36.3	NS
1992	42.3	44.5	NS
Significance of Differences Between years	p = <.001	p = .085	

Table 2. The comparative influence of prewetted plots that were either scalped to remove the cryptobiotic crust along with ~ 1.0 cm of the surface soil or left natural prior to driving over them with a 50 metric ton howitzer. The variable measured was infiltration rate of water into the soil through a single-ring, constant-water-head infiltrometer. Trials were run in August 1992. Treatment occurred in July 1991. There were 12 replications per treatment. Traffic treatments and control plots are pooled for this table.

Wetting Treatment	Treatment	
	Control	Scalped
	Infiltration Rate (ml/5 min)	
Dry	44.5	34.4
Prewetted	42.3	22.3
Significance of Difference	p = <.50	p = .003

Table 3. The influence of variable amounts of 50 ton howitzer traffic on infiltration rates into a clay loam soil at Dugway Proving Grounds, Utah. the howitzer was a track propelled vehicle: 0, 1, 4, or 10 trips were made over plots replicated in 3 randomized blocks in July 1991. The infiltration rates reported here were obtained in August of 1991 and 1992. Prewetted and dry plots are combined for this analysis. Sample size was 6 for each treatment and year. Within any one year, means follows by the same lower case letter do not differ significantly.

No. Vehicular Passes	Infiltration Rate (ml/5 min)	
	1991	1992
0	49.9 ^a	71.1 ^a
1	31.2 ^b	41.3 ^b
4	22.1 ^b	41.1 ^b
10	13.2 ^b	19.8 ^c

Table 4. Relative Colonization of roots by Rhizosymbionts on Cyanobacterial Crusted vs. Comparable soils without a Biotic Crust

<u>Species*</u>	<u>Associate Microbe</u>	Average Percent of Root Length Colonized (N = 5 in each Group)	
		<u>No Biotic Crust</u>	<u>Cyanobacterial Crust</u>
<u>Bromus tectorum</u>	VA Mycor.	3	8
<u>Coleogyne ramosissima</u>	VA Mycor.	5	18
<u>Festuca octoflora</u>	VA Mycor.		
Colorado Plateau		T	1
Washington County		2	4
<u>Lupinus pusillus</u>	Rhizobia	22	34
<u>Plantago patagonica</u>	VA Mycor.	No Sample	13
<u>Stipa hymenoides</u>	Rhizosheaths	40 weak	100 (60% strong)

* Roots of the following species were studied, but no mycorrhizae were observed: Cryptantha pterocarya, Cryptantha crassisepala, Mentzelia albicaulis, and Streptanthella longirostris. All of these species are annuals.

NITROGENASE ACTIVITY, CHLOROPHYLL CONTENT, AND CHLOROPHYLL
DEGRADATION AS INFLUENCED BY MECHANICAL DISTURBANCE OF
CRYPTOBIOTIC SOIL CRUSTS IN A GREAT BASIN DESERT

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³ U.S. Army Corps of Engineers, Construction Engineering laboratory, Champaign, IL 61820

ABSTRACT

Cryptobiotic soil crusts are an important component of semi-arid and arid ecosystems. Two important roles include contribution of fixed nitrogen and carbon to these systems. This study examined the effects of different surface disturbances (raking, scalping, and tracked vehicles) on nitrogenase activity, chlorophyll content and chlorophyll degradation in these crusts one year after disturbance. Any kind disturbance considered was found to reduce nitrogenase activity by 77-97%, with no significant recovery seen after one year. Chlorophyll content was significantly lower in the scalped treatments, but not different among other treatments. Therefore, recovery of this characteristic is fairly quick, unless surface material is removed. Differences in chlorophyll degradation among treatments were not statistically significant. Reasons for rapid recovery of chlorophyll and non-recovery of nitrogenase activity are discussed.

INTRODUCTION

Cyanobacterial-lichen soil crusts are common in semi-arid and arid landscapes of the world, representing over 70% of the living cover in some of these systems. These crusts contribute in many ways to the ecosystems in which they occur. Contributions include enhancement of soil stability by reducing both wind and water erosion. Cryptophyte growth produces microcatchments on soil surfaces which hold water from heavy storms until infiltration occurs, thus reducing runoff erosion. Gelatinous secretions from cryptobiotic cells bind soil particles together and enhance the capacity of soil surfaces to resist both water and wind erosion (Belnap and Gardner 1993; Fletcher and Martin 1948; Kleiner and Harper 1972, 1977; Loope and Gifford 1972; Anderson et al., 1982a, 1982b; Harper and Marble 1990; Shields and Durrell 1964; Anantani and Marathe 1974; Anderson and Rushforth 1976; Campbell 1979; Maranthe 1972; Metting and Rayburn 1983).

Crusts can increase the nutrient status of soils. Many cyanobacteria and cyanobacterial components of soil lichens fix atmospheric nitrogen (Belnap 1992; Skujins and Klubek 1978; West and

Skujins 1977; Terry and Burns 1987; Fuller et al., 1960). Studies utilizing stable isotopes of nitrogen have demonstrated that nitrogen fixed by cyanobacteria in crusts is available to, and used by, neighboring vascular plants (Mayland et al., 1966; Mayland and McIntosh 1966). In some desert systems, these crusts have been demonstrated to be a dominant source of nitrogen used by associated seed plants (Evans and Ehleringer, unpublished data). Plants grown in such crusts show higher levels of many essential macronutrients than plants of the same species grown in uncrusted soils (Harper and Belnap, 1993).

The presence of soil crusts can also affect seedling establishment and survival. Results reported by Harper and Marble (1988) for both fine and coarse-textured soils showed that seedling establishment of several forb and grass species was significantly greater on crusted areas than on sites where the crust had been removed. Survival over a three year period was greater for all species considered on crusted versus scalped soils (Harper, unpublished). Other studies have also reported enhanced seedling germination and establishment on biologically crusted surfaces compared to adjacent non-crusted surfaces (St. Clair et al., 1984).

Trampling negatively affects the integrity and coverage of cyanobacterial crusts, since the filaments are brittle when dry and both the cyanobacteria and lichens are easily crushed (Harper and Marble 1990; Belnap, 1993). Recover of crusts after mechanical disturbance has been studied by several investigators (Anderson et al., 1982b; Jeffries and Klopatek 1987; Callison et al., 1985; Cole 1991). Recovery has been defined in terms of either biomass of cyanobacteria and green algal, or the reestablishment of a visible crust on the soil surface. Recovery rates have been found to depend on the type and extent of disturbance, the availability of nearby inoculation material, and on temperature and moisture regimes that follow disturbance events. Estimates of time for unaided recovery of cryptobiotic crusts from disturbance have varied widely, ranging from a few years to 100 years for full recovery of all components. Belnap (1993) estimated that crusts on sandy soils on the Colorado Plateau require at least 40 years for full recovery under stable soil conditions.

The effects of disturbance on physiological processes in cryptobiotic crusts and on their rate of recovery in natural ecosystems have been neglected. This aspect is physiological functioning of the crusts. This study examines the effects of different kinds of disturbance on nitrogenase activity, chlorophyll degradation and chlorophyll content of cyanobacterial rich soil crusts, and the rate of recovery of each physiological parameter from the different kinds of disturbance.

MATERIALS AND METHODS

Plots were located at Dugway Proving Grounds, Utah. The soil at the study area is a clay loam of lacustrine origin. The vegetation is dominated by Kochia americana and Atriplex confertifolia (5.4% vascular plant cover). The area chosen for study supported a well-developed cyanobacterial-lichen-moss soil crust, with the respective cover for those three groups averaging 11, 24 and 7%. Of the lichens present, only Collema sp. is known to fix nitrogen; it represented >50% of the lichen cover. Of the cyanobacteria present, Microcoleus vaginatus was dominant, often being the only cyanobacterial species present in a sample. The study area had not been trampled by livestock or subjected to vehicular or foot traffic for over 40 years prior to treatment. Treatments were applied in July 1991. Treatments were replicated twice in each of 3 randomized blocks. Treatments included control plots, shallow raking (surface 2 cm), deep raking (surface 10 cm), scalping away the top 1.0 cm of soil, driving over plots with a tracked vehicle (a 50 ton mobile howitzer) 1, 4, and 10 times, and scalping plus howitzer traffic (4 passes). These treatments were applied to dry soils and to soils wetted with the equivalent of 5 cm of rain one day before treatment. Only the dry soil treatments are considered in this report.

Nitrogenase activity and chlorophyll content were analyzed in April, 1992, approximately 9 months after the plots were treated. Samples were collected dry. For nitrogen fixation, 20 samples were collected from each treatment. Samples were collected in 2.5 cm diameter transparent, plexiglass tubes that were open at both ends. Tubes were pushed into the soil surface to isolate an intact sample. Samples were immediately corked at both ends and transported to a mobile laboratory in upright position. The

entire sample was wetted with a constant volume of distilled water on arrival at the laboratory and injected with enough acetylene to create a 10% acetylene atmosphere. After injection, the crust samples were incubated for 4 hours at 26 C in a chamber lighted with Chromo50 (5000 K) and cool white fluorescent bulbs. Subsamples (0.25 ml) of the atmosphere from head space above samples in the tubes were analyzed for concentrations of acetylene and ethylene using a Carle FID gas chromatograph equipped with a 244 cm, 8% NaCl on alumina column, using helium as the carrier gas (30 ml/min).

For chlorophyll measurements, 15 samples per treatment were collected dry as above and extracted immediately. Techniques outlined in Ronen and Galum (1984) were used. Chlorophyll was extracted from samples with dimethylsulfoxide (DMSO) in the dark for 45 minutes at 65 C. Samples were then centrifuged and absorption spectra were measured for the supernatant liquid with a Hewlett-Packard diode array spectrophotometer previously calibrated with a DMSO blank. Optical densities of both acidified (using 1N HCl) and nonacidified extracts were determined by scanning between 700 and 400 nm. Acidified extracts of the cyanobacterial soil crusts showed a drop at OD398 (chlorophyll *a*), and a new peak at OD362 (phaeophytin), and a drop at OD665 (chlorophyll *a* and phaeophytin). Consequently, readings at 362 nm and 398 nm were used to estimate chlorophyll degradation ratios. Readings at 665 nm (chlorophyll *a*) before and after acidification (with 1N HCl), and at 750 for turbidity were used to estimate chlorophyll *a* per unit surface area. Chlorophyll *a* was determined using an equation modified to express pigment content on the basis of surface area:

$$\mu \text{ chl } a \text{ cm}^{-2} = \frac{26.73 (*) (v)}{(A) (L)}$$

where (*) is the difference in absorbance before and after acidification (of 665 nm - 750 nm); (v) is the extract volume in ml; (A) is the surface area of the sample in cm²; and (L) is the path length of the spectrophotometer cuvette in cm. This equation accounts for any phaeophytin or turbidity in the sample (Beymer and Klopatek, 1992). Chlorophyll degradation ratios were constructed by dividing readings at 398 nm by readings at 362 nm. Results were analyzed using analysis of variance (ANOVA) and Duncan's multiple range test.

RESULTS

Results for nitrogenase activity, ranked according to activity levels, are shown in Table 1. The control (T1) shows significantly higher nitrogenase activity levels (35.5 picomoles/hr) than that for any treatment (treatment means ranged from 1.0 to 8.0 picomoles/hr). This represents a 77-97% reduction in nitrogenase activity due to disturbance of the biotic crust, with a mean reduction of 88%. Treatment means did not differ significantly from each other.

Chlorophyll content differed significantly between the two scalped treatments nor between the shallow raked and the one-pass only treatments. As would be expected, the scalped treatments had less chlorophyll than other treatments. The remainder of the treatment means did not differ significantly from each other. Chlorophyll degradation showed no significant differences among treatments (Table 2).

DISCUSSION

All of the disturbance treatments greatly reduced nitrogenase activity in the biotic crusts. Even though this study was done 9 months after the initial disturbance, nitrogenase activity was much suppressed for all treatments relative to the control.

Several nitrogen-fixing species were present in these crusts before disturbance. The lichen Collema sp. is known to be an active fixer (Belnap, 1992). However, this lichen is very sensitive to both trampling and burial by sediments. When dry, it is brittle and easily broken by compressional forces, and small pieces of the thallus may be blown away or buried as the crust is mechanically disturbed by any procedure tested here. Even if pieces are left on the surface, nearby disturbances may create enough wind- or water-borne sediments to bury them. Since this lichen generally cannot grow quickly enough to reach the surface before exhausting its resources, burial often results in death. Consequently, most mechanical disturbances would result in a reduction of this lichen's ability to fix nitrogen and contribute chlorophyll to the soil on which it grows.

Soil cyanobacteria are also capable of nitrogen fixation. Although several known nitrogen fixers were identified in the crust sampled, the only species with a significant amount of biomass was the cyanobacterium Microcoleus vaginatus. This cyanobacterium has multiple filaments contained within an extracellular sheath (Fig. 1). It is a non-heterocystous species, but it is known to fix nitrogen in soils throughout the Colorado Plateau (Belnap, 1992). It is not known how the oxygen exclusion necessary for nitrogen fixation is accomplished in this species without heterocysts. It is possible that an anaerobic environment develops either within the sheath itself, or more likely, that groups of sheaths packed together are able to exclude free oxygen. This packing could be accomplished by sheaths with or without living filaments inside. If this is true, then virtually any disruption of the tightly packed filament could create an oxygenated environment and stop nitrogen fixation. Since the structure of these crusts is extremely fragile, especially when they are dry and the sheath material is brittle, virtually any surface disturbances would result in a cessation of nitrogen fixation.

Most cyanobacteria are much more tolerant of burial than soil lichens. M. vaginatus can move readily through soils when they are wetted, often traveling up to 5 cm in 24 hours (S. Campbell, personal communication). This enables them to reach photic zones even when covered by water- or wind-borne sediments. Given those abilities, it is not surprising that one-time surface disturbances that did not actually remove the biotic crust did not significantly reduce chlorophyll levels. Scalped plots, where the biotic crust was removed, would be expected to have lower chlorophyll contents until enough time had passed for the photosynthetic microbial populations to re-establish themselves. Since these organisms are only active when wet, recovery time for chlorophyll content of soil would be heavily dependent on rainfall.

Recovery of nitrogenase activity in Collema - M. vaginatus dominated systems, however, obviously takes much longer than recovery of chlorophyll content on the same sites. Since the amount of chlorophyll present is not significantly different between control and treatment plots, but nitrogenase activity is greatly different, nitrogen fixation is clearly not determined by the number of cyanobacterial

cells present only. If nitrogenase activity in Mycrocoleus is dependent in some way on packing of its filaments, recovery of N-fixation activity may be more closely related to the production of sheath material and/or new filaments. Likewise, little is really known about rates of production for either of these components. Sheath material is produced whenever this cyanobacterium is wetted and its filaments extruded (Belnap, personal observation), but there is no information on rates, or what controls them. Nothing is known about what controls the production of filaments, or what determines the number of filaments per sheath. It has been noted that the number of filaments per sheath tends to be higher in gypsiferous and limestone soils, as well as in sandy soils that have not been subjected to trampling by livestock or humans (Belnap, 1992).

This study raises many questions critical to management of semi-arid landscapes. These ecosystems naturally maintain little nitrogen in readily available forms, and any activities that adversely affect availability of this often-limiting element may affect the productivity and long-term health of all living components of the system. Research is needed to understand the mechanisms controlling nitrogenase activity in cryptobiotic crusts and how mechanical disturbance affects that activity. With such information available, managers could control actions that damage cryptobiotic crusts and implement actions that hasten their recovery.

Acknowledgments: This work was supported by a subcontract from the Shrub Sciences Laboratory, Intermountain Research Station, U.S. Forest Service at Provo, Utah. The contract was funded by the U.S. Army Corps of Engineers, Construction Engineering Laboratory, Champaign, Illinois.

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Table 1. Nitrogenase activity in surface soils that received the listed treatments 9 months earlier. Nitrogenase activity in control samples was significantly greater than that for all other treatments ($p < 0.02$). Means followed by the same lower case letter do not differ significantly.

Treatment	Nitrogenase Activity (Picomoles/hr)
Control	35.5 a
Deep raked	8.0 b
One pass	5.3 b
Shallow raked	4.0 b
Ten passes	3.8 b
Scalped, four passes	2.9 b
Four passes	2.3 b
Scalped	1.0 b

Table 2. Chlorophyll contents and chlorophyll degradation ratios for the treatments listed. Means followed by different letters differ significantly ($p < 0.05$). No significant differences were found among the chlorophyll degradation ratios.

Treatment	Chlorophyll Content $\mu\text{g}/\text{cm}^2$	Chlorophyll Degradation OD362/OD398
One pass	5.3 a	.94
Shallow raked	4.8 a	.95
Control	4.2 a	.98
Ten passes	3.0 a	.95
Deep raked	2.6 a	.91
Four passes	1.1 b	.96
Scalped	1.0 b	.99
Scalped, four passes	1.0 b	.96

THE INFLUENCE OF CRYPTOBIOTIC SOIL CRUSTS ON ELEMENTAL CONTENT OF
TISSUE ^{of} IN TWO DESERT SEED PLANTS

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ABSTRACT

Soil surface growths dominated by cyanobacteria and the lichen Collema in southeastern Utah are shown to be associated with greater tissue content of several bioessential elements in two co-occurring seed plants (Festuca octoflora, Poaceae, and Mentzelia multiflora, Loaceae). The elements N, P, K, Ca, Mg, and Fe were present in significantly greater concentrations in Festuca growing on heavily crusted soils than in plants on the same soil where foot traffic had destroyed the cryptobiotic crusts. With Mentzelia, N, Mg and Fe were present in significantly greater concentrations in plants from sites with crusted soil surfaces than on blow sand sites. The cryptobiota appeared to compete vigorously with Mentzelia for available P: Mentzelia plants from crusted sites contained significantly smaller concentrations of P than plants grown on soils where wind action precluded development of surface crusts.

These cryptobiotic crusts fix considerable amounts of N, which apparently becomes available to associated seed plants via decomposition and cellular secretion processes. Other macronutrients are apparently accumulated in forms available to seed plants as the crusts develop in interspaces between higher plants. The trace element Fe appears to be rendered more available to higher plants by the cryptobiotic growth. That effect may be related to chelating compounds known to be present in the mucilaginous sheaths of cyanobacteria. Other possible reasons for the enhanced nutrient uptake of seed plants growing in cryptobiotic crusts are discussed.

Cryptobiotic crusts consisting of cyanobacteria, various algae, lichens, mosses, and heterotrophs such as microfungi and bacteria are conspicuous components of the surfaces of desert soils worldwide (West, 1990). Many influences have been ascribed to these crusts in semi-arid and arid regions. Suggested influences have included reduction of water runoff, reduced sediment production from both wind and water, and addition of organic matter and nitrogen to associated ecosystems (Harper and Marble, 1990; Shields and Durrell, 1964; Belnap and Gardner, 1992).

Some attention has been given to the role these crusts play in the nutrition of vascular plants. Most of that attention has centered around the capability of components of the crusts to fix nitrogen in otherwise nitrogen-poor systems. Studies utilizing stable isotopes of nitrogen have demonstrated that nitrogen fixed by cyanobacteria in the crusts is available to neighboring vascular plants (Mayland et al., 1966; Mayland and McIntosh, 1966; Stewart, 1967).

There are indications that cryptobiotic crusts may influence availability of other essential nutrients as well. Kleiner and Harper (1972, 1977) noted more extractable phosphorus in soils supporting cyanobacterial cover than in nearby soils that lacked cyanobacterial cover. Fletcher and Martin (1948) reported that crusts trapped soil fine particles, which are more nutrient-rich than sand (Black, 1968). Lange (1974) demonstrated that compounds in the gelatinous sheath material of half the cyanobacterial species studied were able to chelate elements essential for their growth (e.g., iron, copper, molybdenum, zinc, cobalt, and

manganese). Four of the five genera shown to possess this ability (Anabaena, Anacystis, Lyngbya, and Nostoc) are represented by common species in the cryptobiotic crusts of western North American deserts (Durrell, 1959; Shields and Durrell, 1964). Marble and Harper (1992) showed that scalping away a shallow (1.0 cm) layer of the cyanobacterial crusts from around individuals of a short-lived mustard herb significantly reduced the tissue content of several essential minerals.

This study examines the effect of the presence of cryptobiotic crusts on tissue nutrient content of two species of native seed plants. We compare the elemental content of plants growing on crusted soils with individuals of the same species growing on adjacent soils of similar origin, microenvironment and texture on which cryptobiotic crusts had not developed to obtain an integrated evaluation of possible effects of such crusts on nutrient status of associated plants.

METHODS

Plant tissue of the native annual grass, Festuca octoflora, and the native perennial dicotyledonous herb, Mentzelia multiflora, were chosen for study (nomenclature follows Welsh et al. 1987). F. octoflora was collected from a site approximately 20 miles (33 km) southwest of Moab, Utah. M. multiflora was collected from Arches National Park, 10 miles (17 km) northeast of Moab, Utah. Both areas have been protected from domestic livestock grazing for over 10 years.

Plants were collected from two immediately adjacent sandy sites; one area had well-developed cyanobacterial-Collema lichen crusts, while the other lacked such a crust. At Arches, windblown sand accounted for the lack of crust; at the F. ocotoflora site, the lack of crust was due to repeated trampling by people over a period of years. A composite sample of at least five individuals (or 2.0 g tissue for the tiny Festuca plants) were collected at each of 5 locations for each soil surface condition class at each site. Two composite samples of the surface 3.0 cm of the soil profile were collected from each soil surface class at each site.

Soils were analyzed for percent sand using a hydrometer procedure (Bouyoucous 1936). Soil reaction was determined with a glass electrode on a saturated soil/distilled water slurry. Organic matter was determined by wet digestion in 1.0 N potassium dichromate (Moodie et al., 1963), Total nitrogen in soils was estimated using a micro-kjeldahl procedure (Association of Official Analytical Chemist, 1980). "Available" phosphorus was extracted in 0.2 N acetic acid and determined using the iron-TCA-molybdate method (Goldenberg and Fernandez, 1966). Exchangeable bases were displaced from the soil with 1.0 N ammonium chloride and concentrations in the extraction solution were determined using an atomic absorption unit (David, 1960).

Air dried plant samples (whole plants including major roots remaining when individual plants were pulled up) were cleaned of adherent sand and ground through a 40 mesh sieve using a rotating mill. Samples were stored until analyzed in capped plastic vials. Nitrogen was determined by micro-kjeldahl procedures. A single 1.0

g sample of each specimen was fully digested using a sulfuric acid-nitric acid procedure (1:5 parts respectively of the concentrated acids). Elemental content of essential minerals was determined on aliquots of the digestate using an atomic absorption unit and appropriate analytical procedures (Association of Official Analytical Chemists, 1980). Results of tissue analyses for individual elements were compared using an unpaired t-test model.

RESULTS

At sites where F. octoflora was collected, characteristics of the crusted and uncrusted soils were similar in both texture and chemical characteristics (Table 1). The most notable differences were higher levels at crusted sites for organic matter (1.14 vs. 0.49%) and nitrogen (0.043 vs. 0.024%). Zinc (0.6 vs. 0.2 ppm) and iron ((0.6 vs. 1.2 ppm) showed differences between the two soil surface types, but values for both elements are so low that minor differences in aggregates included in the soil subsample drawn for the analyses could account for observed elemental differences.

Mineral composition of Festuca octoflora varied significantly between crusted and uncrusted soils (Table 2). For all essential nutrients measured (Mn excepted), there were greater amounts in plants from crusted areas. Observed differences were statistically significant ($p < 0.05$ or better) for all the macronutrients measured (N, P, K, Ca, and Mg) and for the micronutrient Fe (Table 2). Of the essential elements, Fe showed the greatest difference, with levels in plants from crusted areas twice that of plants from

uncrusted soils (300 vs. 149 ppm). Considering the difference in Fe in the two soils (Table 1), such a large difference in tissue content was unexpected. Phosphorus levels in plants from crusted areas were 79% higher than for plants from uncrusted areas (0.25 versus 0.14%), but the crusted soils contained more phosphorus than blow sand in roughly the same proportions as observed in tissue from the two sites. Calcium levels in plants from crusted areas were 25% higher than in blow sand (0.65 vs. 0.52%). Potassium, Mg and N were all 15% higher in plants from the crusted areas than those grown on the uncrusted blow sand (1.88 vs. 1.64; 0.15 vs. 0.13; 2.25 vs. 1.95 ppm, respectively). The difference in tissue content of K and N could have been predicted from content of those elements in soil, but Mg may have been more efficiently taken up on the crusted surfaces, since those soils showed less chemically extractable Mg than blow sands. Since the soil sample size was small, however, statistical significance cannot be attached to this result. Copper, Mn, Na and Zn levels in the plant did not differ significantly between the two sites.

Soil samples from the two surface types from which Mentzelia plants were collected were texturally similar, but they differed greatly in respect to certain chemical parameters (Table 3). Organic matter, N, P, K, Ca, Mg, Mn and Zn were much higher in the crusted soils. Results for Mentzelia multiflora tissue analyses were similar to those for Festuca octoflora, although fewer elemental differences were statistically significant (Table 4). All macronutrients except P were in greater concentrations in plants from crusted areas, as might have been expected given the

larger amounts of those elements in crusted soils. However, only the differences for N and Mg were statistically different.

Although exchangeable Fe was less abundant in the crusted soils (Table 4), Fe content in Mentzelia was significantly greater in tissue from soils topped by a cyanobacterial-Collema crust. This pattern is consistent with that observed for F. octoflora and may indicate that the gelatinous secretions of associated cyanobacteria render Fe more available to both the cyanobacteria and to Mentzelia. Sodium also was in statistically greater amounts in plants from crusted areas.

DISCUSSION

In deserts of the Colorado Plateau, soil crusts are dominated by the cyanobacterium Microcoleus vaginatus and the soil lichen Collema tenax which takes Nostoc as its phycobiont. Both of these organisms fix atmospheric nitrogen and stabilize the surface soil (Belnap, in manuscript; Belnap and Gardner, 1992). Since both clay particles and organic material are negatively charged, they will electrostatically adsorb positively-charged essential nutrient ions and hold them in a form available to higher plants (Lange, 1976; Black, 1968). Since most of the organic matter in the crusted sands considered in this study appears to be produced by the cryptobiotic taxa, they are probably exerting a strong influence on availability of both nitrogen and the cations essential to the metabolism of associated vascular plants. The effects are almost certainly most profound for annual plants of small stature (such as

F. octoflora) which deploy most of their rooting volume in a zone that is greatly influenced by the cryptobiotic taxa that constitute the biological crusts that are so common in these deserts. Deeper rooting, herbaceous perennial herbs (such as M. multiflora) should also experience some beneficial nutritional influences from the crusts, especially during the establishment phase. Many of these species, including M. multiflora, have extensive surface root mats during the spring (Belnap, personal observation) which would enable these plants to take advantage of the crusts' nutritional benefits during the time both the crusts and the plants are most active. Deep rooting, long-lived shrubs may show less influence from associated cryptobiotic crusts during most of their lifespan, but such an influence may be observable and ecologically important during seedling germination and establishment.

Nitrogen was in greater concentrations in both of the seed plants investigated in this study when they occurred on crusted soils. Additional N would be available to plants in crusted areas from two sources. First, the two dominant organisms of the crusts at the collection sites, Microcoleus vaginatus and Collema tenax both fix atmospheric N. The ability of vascular plants to take advantage of nitrogen fixed by these crusts has been demonstrated by several authors (Mayland et al., 1966; Mayland and McIntosh, 1966; Stewart, 1967; Fuller et al., 1960). Secondly, nitrogen would be made available through the death and decomposition of crustal species.

Iron was significantly higher in both species of seed plants when they grew on crusted areas. Since more iron was available in the uncrusted soils, it seems probable that the cryptobiotic crust

somehow make Fe more available to at least the vascular plant species considered here. M. vaginatus produces an extraordinarily thick, extracellular, gelatinous sheath. The sheath material may be distributed throughout up to 10 cm of sand below undisturbed crustal surfaces, and that sheath material may enhance the availability of Fe throughout its zone of influence. Chelation of iron is especially important in alkaline soils, such as those considered in this study, since iron is otherwise bound in chemical forms unavailable to vascular plants on such soils (Wallace 1956).

The presence of any organic material contributed by the cryptobiotic taxa might contribute to increased nutrient availability in other ways as well. Since the sheath materials are sticky when wet, fine clay particles are readily incorporated into cryptobiotic surfaces and protected from wind erosion when the soils dry. As both the sheath materials and the clay particles have slight negative charges, positively charged nutrient cations would be adsorbed on particles in a form readily available to vascular plants. The sheath materials also bind soil particles together, thus producing water stable aggregates that are resistant to both wind and water erosion (Belnap and Gardner, 1992; Bond and Harris, 1964; Bailey et. al., 1973). Schulten (1985) has shown that mosses also enhance soil aggregation, even though they do not secrete gelatinous exudates into the environment. Such aggregation processes would also keep soil fine particles in upper soil horizons, rather than letting them be washed downwards by percolating water.

Soil samples from the two surface types from which Mentzelia plants were collected differed greatly. Organic matter and N content were expected to vary widely in the two surface types, because of the activity of associated autotrophic microbiota. Greater amounts of K, Ca, Mg, Fe, Mn, and Zn may have been held in crusted soils as electrically adsorbed cations on clay particles trapped in the gelatinous secretions from cyanobacterial components of the crusts or as cations electrostatically held on the surfaces of organic matter. Among the trace elements, Mn, Na and Zn were much more abundant in the crusted surface soil, while exchangeable Fe was most abundant in the blowsand. The results for the first three trace elements suggest that they are primarily associated with finer soil particles and organic matter. The low values for Fe in the crusted surface may be related to uptake of that element by the microbial components of the crust.

Other aspects of the crusts may play a useful role as well. Since crusted surfaces are roughened, wind-borne soil particles would more easily lodge in crusted areas, and such fine particles are often more nutrient-rich than sand (Black, 1960). Well-developed soil crusts are also much darker than non-crusts areas. As a result, surface soil temperatures could be expected to be warmer, and chemical reactions and metabolic rates of associated organisms would be faster in late fall, winter and early spring when usable moisture is most likely to be available in the region considered here. Warmer soil temperatures may result in increased uptake of essential minerals from the soil, since increasing

temperature is tightly linked to metabolic rate as is mineral uptake (Salisbury and Ross, 1985).

Phosphorus in plants from crusted areas was found to be significantly lower in Mentzelia and significantly higher in Festuca relative to plant content when grown on uncrusted soil. Crusted soils at both sites contained approximately the same amount of P (80.6 and 82 ppm), and test plants from those soils contained about the same relative content of this mineral (Mentzelia, 0.20%; Festuca, 0.25%). In contrast, there was significantly more P in Mentzelia plants grown on uncrusted sand than in plants from the crusted site, even though there was much less extractable P in the uncrusted soil (30.6 ppm). Such data argue strongly for competition between the cryptobiotic flora and Mentzelia for P. Data available from an unpublished study in our laboratory demonstrate that the cyanobacteria, which occur in the top 5 mm of soil, compete vigorously with vascular plants for minerals when conditions for cyanobacterial growth is good (Harper and Belnap, unpublished). Examination of Mentzelia root systems at the crusted and uncrusted sites in March, 1992, revealed a dense mesh of feeder roots in the surface 1.0 cm of sand. Competition between Festuca and the cryptobiotic flora for P was not apparent.

No consistent correlation could be found between levels of minerals in the plant tissues and levels of the same elements in associated soils in this study. There are apparently significant differences in the physiology of essential nutrient uptake between the two plant species considered here. That would not be surprising, since Festuca is a monocot and Mentzelia is a dicot,

and large differences in nutrient uptake by roots produced by monocots and dicots have often been documented (Woodward et. al., 1984).

Another study has also shown nutrient enhancement in seed plants grown on crusted soils. In a study of the biennial Lepidium montanum growing on crusted clay soils, the surface 1.0 cm of crusts was scalped away in a 20 cm radius around young plants in the rosette stage. After 3 months, when plants had flowered, all above-ground parts were harvested. Plants growing in areas without crusts had significantly lower levels of potassium, magnesium, copper, and sodium. They also had 30% less average dry weight (Marble and Harper, in manuscript). No minerals were found to be in higher concentrations in plants growing on uncrusted soils.

Much additional work is needed to establish the relationship between vascular plants' nutrient status and the presence of cryptobiotic crusts. More plants species should be analyzed for mineral content to determine how widespread the phenomenon of cryptobiotic enhancement of essential nutrient uptake by associated seed plants is. Other experiments are needed to identify factors that are responsible for the observed increase in nutrient uptake by intermixed vascular plant.

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Table 1A. COMPARISON OF SOIL CHARACTERISTICS ASSOCIATED WITH CYANOBACTERIAL - COLLEMA STABILIZED SOILS VERSUS BLOW-SAND AT THE WIND WHISTLE SITE, SAN JUAN COUNTY, UTAH.

CHARACTERISTIC	CYANOBACTERIAL- <u>COLLEMA SAND</u>	BLOW <u>SAND</u>
SAND (%)	79.7	87.8
REACTION (pH)	7.6	7.7
	<u>%</u>	
ORGANIC MATTER (%)	1.14	0.49
NITROGEN (%)	0.043	0.024
	<u>PPM AVAILABLE OR EXCHANGEABLE</u>	
PHOSPHORUS	82.0	51.6
POTASSIUM	92.8	75.2
CALCIUM	3,840.0	3,040.0
MAGNESIUM	90.0	100.0
COPPER	0.2	0.2
IRON	0.6	1.2
MANGANESE	14.2	7.8
SODIUM	9.6	9.6
ZINC	0.6	0.2
SAMPLE SIZE	2	2

Table 1 B, COMPARISON OF SOIL CHARACTERISTICS ASSOCIATED
WITH CYANOBACTERIAL - COLLEMA STABILIZED SOILS
VERSUS BLOW-SAND AT THE COURTHOUSE WASH DUNES,
GRAND COUNTY, UTAH.

<u>CHARACTERISTIC</u>	<u>CYANOBACTERIAL- COLLEMA SAND</u>	<u>BLOW SAND</u>
SAND (%)	85.7	92.9
REACTION (pH)	7.5	7.6
	<u>%</u>	
ORGANIC MATTER	0.71	0.23
NITROGEN	0.025	0.006
	<u>PPM AVAILABLE OR EXCHANGEABLE</u>	
PHOSPHORUS	80.6	30.6
POTASSIUM	61.4	38.0
CALCIUM	4,100	1,610
MAGNESIUM	60.0	30.0
COPPER	0.2	0.2
IRON	0.6	2.2
MANGANESE	20.4	5.8
SODIUM	9.6	6.4
ZINC	0.6	0.2
SAMPLE SIZE	2	2

Table 2. MINERAL COMPOSITION OF TISSUE OF FESTUCA
OCTOFLORA WALTER GROWN ON CYANOBACTERIAL
AND LICHEN STABILIZED SAND VERSUS BLOW SAND
WITHOUT CYANOBACTERIA AND LICHENS.

<u>CHARACTERISTIC</u>	<u>CYANOBACTERIAL- LICHEN SOIL</u>	<u>BLOW SAND</u>	<u>SIGNIFICANCE OF DIFFERENCE</u>
<u>SAMPLE SIZE</u>	5	5	---
	<u>% BY WEIGHT</u>		
NITROGEN	2.25	1.95	*
PHOSPHORUS	0.25	0.14	***
POTASSIUM	1.88	1.64	*
CALCIUM	0.65	0.52	***
MAGNESIUM	0.15	0.13	**
	<u>PPM</u>		
COPPER	11.0	10.4	NS
IRON	300.3	149.4	*
MANGANESE	60.3	74.0	NS
SODIUM	61.5	59.8	NS
ZINC	43.0	33.0	NS

*** - $P < 0.001$; ** - $P < 0.01$; * - $P < 0.05$

Table 3. MINERAL COMPOSITION OF MENTZELIA MULTIFLORA
(NUTT.) GRAY TISSUE GROWN ON CYANOBACTERIAL -
COLLEMA STABILIZED SAND AND ASSOCIATED BLOW-
SAND.

CHARACTERISTIC	CYANOBACTERIA- COLLEMA SAND	BLOW SAND	SIGNIFICANCE OF DIFFERENCE
SAMPLE SIZE	5	5	---
	<u>% BY WEIGHT</u>		
NITROGEN	2.61	2.18	* *
PHOSPHORUS	0.20	0.24	* *
POTASSIUM	3.04	2.67	NS
CALCIUM	2.50	1.97	NS
MAGNESIUM	0.33	0.23	*
	<u>PPM</u>		
COPPER	8.6	9.0	NS
IRON	639.8	465.4	*
MANGANESE	98.2	82.4	NS
SODIUM	77.2	63.4	*
ZINC	22.0	20.0	NS

* - $P < 0.5$; NS = NOT SIGNIFICANT

EFFECTS OF DISTURBANCE BY TRACKED VEHICLES ON WIND AND WATER EROSION



A Report Submitted to

The U.S. Forest Service
Intermountain Forest and Range Experiment Station
Shrub Sciences Laboratory
Provo, UT 84601

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ABSTRACT

Surface crusting by physicochemical and biological processes such as the formation of vesicular porosity and microphytic surfaces [syn: cryptogams], respectively, is a common feature of non-tilled, extensively managed arid and semi-arid soils. This study was conducted to determine the affects of tracked vehicles on the soil stability afforded by microphytic crust. Soil stability was indexed by infiltration capacity and wind velocity thresholds for surface disruption. The effects of eleven surface disturbance treatments, the undisturbed soil surface found in shrub interspaces, disturbance of the surface by one, four, and ten passes of a tracked vehicle in both wet (2.48 cm applied as a depth equivalent volume) and air-dry conditions, microphytic crust carefully removed with a trowel ("scalping"), shallow raking to a depth of 2.5 cm with a steel garden rake to disturb microphytic crust, and deep raking to a 7.5 cm depth to disturb both microphytic and vesicular crust. Response of infiltration capacity to the treatments in this study was related to the number of disturbance repetitions. Ten passes of the tracked vehicle alone, and scalping the plot prior to ten passes reduced infiltration capacity after 45 minutes and time to runoff to the greatest extent, while concomitantly increasing suspended sediment concentration. Deep raking to disturb the vesicular horizon, and thereby potentially improve infiltration characteristics, actually reduced infiltration capacity and time to runoff when compared to controls. Removal of the microphytic crust reduced infiltration capacity. Shallow raking, while retaining some of the microphytic crust structures seemed to have similar infiltration capacities and sediment concentration as the undisturbed controls.

INTRODUCTION

Recent efforts by the U.S. Department of Defense (DoD) to comply with environmental statutes on military installations has resulted in a renewed interest in the effects of tracked vehicle disturbance on soil stability. Military activities in the Great Basin Physiographic Province provide the potential for site disturbance, with associated vegetation removal, accelerated soil loss, and excessive surface runoff. Rehabilitation or restoration of these disturbed sites may be influenced by the propensity of the native soil to form soil crusts and other impediments to infiltration and percolation. Formation or disturbance of these crusts may reduce or improve surface soil moisture movement, thereby affecting the reestablishment of a vascular plant cover.

On non-tilled, extensively-managed wildlands in arid to semi-arid regions, crusts of various compositions and compactions often form at the soil surface. Three broad categories of crust formed in arid soils include physicochemical, mechanical, and biological crusts (Skujins, 1975; Isichei, 1980). This study will focus on the physicochemical *vesicular* crusts and the *microphytic* (syn: cryptogamic) biological crusts at the soil surface.

PREVIOUS WORK

Physicochemical Vesicular Crusts

Soil crusts develop in the top few millimeters of almost every soil. This layer is often characterized by its hardness, horizontal orientation of soil particles, high bulk density, low organic matter and high silt contents. High sodium contents aggravate this problem (Kemper

and Miller 1978). Vesicular porosity or "foam" soils, consisting of spherical or elliptical vesicles often form near the soil surface as a horizon several centimeters thick. Vesicular pores are macroscopic and unconnected (Miller 1971). This vesicular horizon is usually overlain by rock pavement, a thin soil crust or a biological crust (Springer 1958, Hugie and Passey 1964, Evenari et al. 1974), particularly on playas used for military maneuvers. In the Intermountain region, soils with vesicular porosity are associated with cold-desert shrub plant communities with little herbaceous vegetation in the understory or shrub interspaces. Eckert, Jr. et al. (1989) has clarified the nature of soil surfaces associated with the spatial distribution of shrubs and shrub interspaces (Fig. 1). Soil texture of these surface horizons are dominated by wind-deposited silt and very fine sand. Formation of these horizons is attributed to the interaction of silt-dominated soils and climatic conditions with a propensity for alternate wetting and drying (Lapham 1932, Hugie and Passey 1964).

The crusting interspace surfaces with high silt, low organic matter, massive structure with vesicular pores contribute to an unfavorable environment for seedling emergence and establishment (Wood et al. 1978, Wood et al. 1982). The surface tends to slake when saturated, followed by drying to a hard crust that impedes coleoptile emergence and radicle penetration (Taylor 1971, Eckert, Jr. et al. 1989). Vesicular horizons are thought to slow the infiltration process and promote sediment production (Blackburn 1975), though the decreased infiltration capacity may depend upon the stage of vesicle development (Miller 1971, Sun 1992).

Vesicles remain gas-filled even under saturated conditions, thereby reducing the cross-sectional

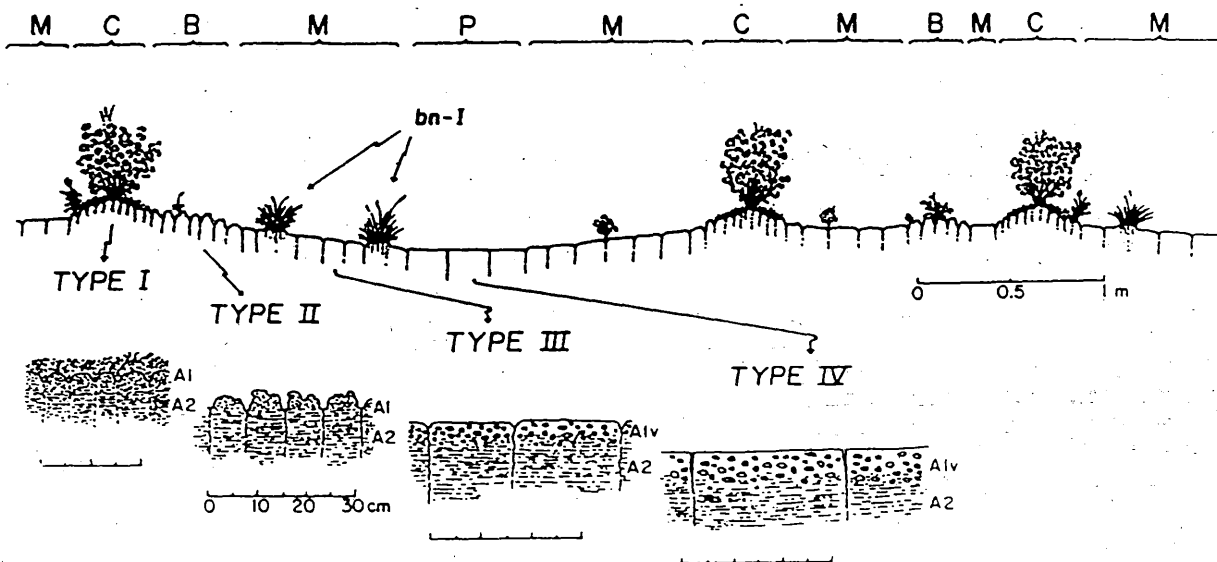


Figure 1. Schematic cross-sectional diagram of the microtopographic positions of four soil-surface types. Bunchgrass-Type I (bn-1) is associated with gently sloping silt dominated soils. Microtopographic positions include: C = coppice dune, the mounds of windblown soil and litter beneath shrubs, B = coppice bench, M = intercoppice microplain, P = playette. Vertical scale is somewhat exaggerated. Type I is typically litter covered. Circles and ellipses indicate vesicular horizons (redrawn from Eckert et al. 1989).

area available for soil wetting (Miller 1971, Evenari et al. 1974). Miller theorized that vesicle size and total pore volume as vesicle increased with continued wetting and drying. Sun found that vesicle increased in number rather than size in some soils. Vesicular porosity can be reproduced by repeatedly wetting and drying a pulverized vesicular horizon or silt-dominated soil.

Biological/Microphytic Crusts

Crusts of biological origin are often formed as a complex of mosses, lichens, liverworts, algae, fungi, and bacteria at the soil surface (Campbell, 1979). These crusts have been described as microfloral (Loope and Gifford, 1972), microphytic (Cameron, 1978), cryptogamic (Skujins, 1984), and organogenic (Evenari, 1985). West (1990) prefers the term microphyte which permits a uncomplicated separation of the terrestrial vegetation into micro- and macrophytic members. Microphytic crust often tops or is combined with physicochemical and mechanical crusts (Isichei, 1980; 1990) and are most conspicuous in open shrubland and grassland of semiarid environments (Metting 1991).

Raindrop impact on exposed mineral soil produces pressure and shear forces which detach soil particles, initiating the process of erosion (Foster et al., 1985). Microphytic crusts are also attributed with the ability to decrease the kinetic energy of raindrops and are considered on poor condition wildlands to be more desirable than bare soils for reducing splash erosion (Osborn, 1952). Early researchers such as Booth (1941) reported the effectiveness of microphytic crust in trapping and binding soil particles, resulting in readily observable

reduction of sediment movement during flash flooding. Fletcher and Martin (1948) and Marathe (1972) found cyanophytic crusts to retain silt and clay. Microphytic crusts are often assumed to reduce wind and water erosion (Alexander, 1969; Fuller, 1974; Crawford and Gosz, 1982; 1986; Rushforth and Brotherson, 1982; Mucher et al., 1988; Harper and Marble, 1988; Campbell et al., 1989), although this literature stresses positive influences in some cases and negative influences in others (West 1990). The different findings are likely due to the variable composition of the crusts, variable soils, and differences in the degree and timing of treatments. Often the effects of microphytic crust are integrated with physical and chemical features of the soil features that also influence erodibility.

In this study simulated rain and wind were used to test the influence of surface disturbance by tracked vehicles and hand raking on the detachment and transport components of the erosion process. Splash from the crown-like ring of droplets carries detached particles radially and upward. Net downslope movement occurs from rain splash alone if a slope exists. In semiarid and arid environments the presence of microphytes may reduce the erodibility of the soil surface and enhance recovery of site productivity and stability (West, 1990). No direct studies are known to exist that have established threshold rainfall intensities for destabilization of microphytic crust resulting in splash erosion.

Specific objectives of this study were: 1) to determine the effects of tracked vehicle disturbance on the integrity of microphytic crusts, and indexed by wind and water erosion; 2) to attempt to distinguish between the effects of disturbance on microphytic crust from

disturbance effects on the underlying vesicular horizon; 3) to examine the influence of antecedent moisture condition on the level and longevity of surface soil disturbance; and 4) to determine the effects of tracked vehicle disturbance on the rate of recovery of microphytic crusts. This report considers objectives one through three. Objective four is under the purview of Dr. Kimball Harper at Brigham Young University.

MATERIALS AND METHODS

Study Area

Research was conducted at the Dugway Proving Ground, southwest of Tooele, Utah (T7S, R11W) (Fig. 2). The area has been protected from grazing for at least 45 years. Dugway is semiarid with mean annual precipitation of 229 mm, coming primarily as winter snow and spring rainfall. Rainstorm intensities vary from 1 to 8 mm h⁻¹. Temperatures range from -4° to 40°C with mean annual evaporation estimated at 17 mm. Vegetation is an association of shadscale (*Atriplex confertifolia*), annual grasses (primarily *Bromus tectorum* L.), and forbs (primarily *Halogeton glomeratus* C.A. Mey). Direct correlation between the cover of perennial chenopod shrub such as *Atriplex* and microphytic crust indicates that the crusts provide spatial concentrations of moisture and nutrients into the surface 100 mm of soil, favoring seedling establishment (Graetz and Tongway 1986).

Soil samples are classified as Swinger Silt Loam (Soil Conservation Service, unpublished), defined as fine-silty, mixed (calcareous) mesic Typic Torriorthents (Morris, 1961; Stephens and Sumsion 1978). Vascular plant cover is an association of shadscale (*Atriplex*

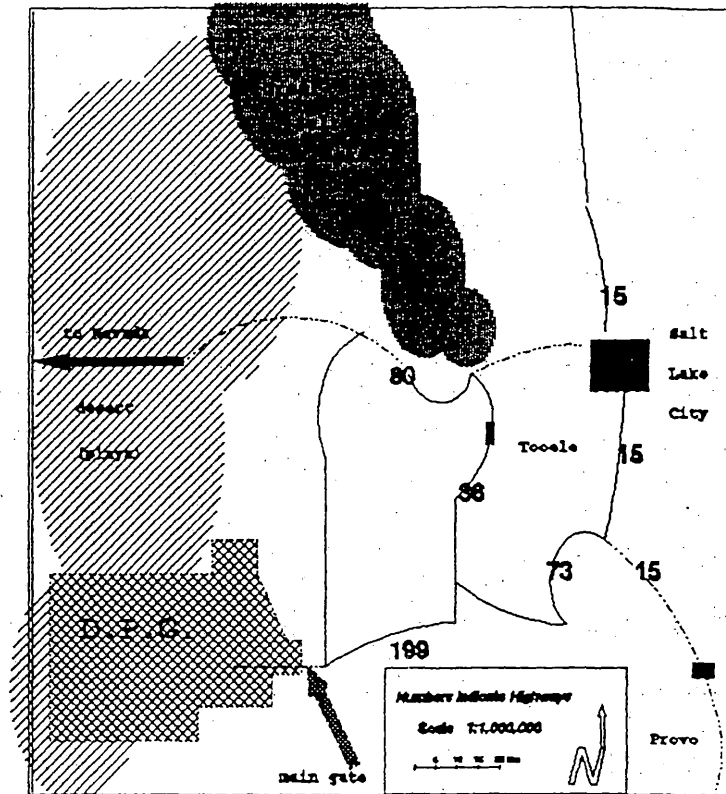


Fig. 2--General location of Dugway Proving Ground, Utah.

confertifolia), grey molly (*Grayia spinosa*), and greasewood (*Sarcobatus vermiculatus*). Cracks on the soil surface are commonly stabilized by microphytes and create a varied microrelief (Anderson et al. 1982, Eckert et al. 1986). Autotrophic microphytes identified on soil in this experiment include green algae (division Chlorophyta), golden brown algae (division Chrysophyta) and filamentous cyanophytes (cyanobacteria) (Harper and Marble, 1988), lichens (primarily *Dermatocarpon hepaticum*), and mosses (principally *Desmatodon plinthobius* and *Tortula intermedia*) (Mason 1969; Flowers 1973; Anderson and Rushforth 1977).

Disturbance Treatments

Prior to the application of surface disturbance treatments, all woody vegetation was clipped to the mineral soil surface to assist plot placement and eliminate the influence of incorporated woody debris. Eleven treatments were applied to the surface soil in three replications. Treatments included the undisturbed soils surface found in shrub interspaces, disturbance of the surface by 1, 4, and 10 passes of a tracked vehicle in both wet (2.48 cm applied as a depth equivalent volume) and air-dry conditions, microphytic crust carefully removed with a trowel ("scalping"), shallow raking to a depth of 2.5 cm with a steel garden rake to disturb microphytic crust, and deep raking to a 7.5 cm depth to disturb both microphytic and vesicular crusts (Table 1). The tracked vehicle was a M-110 Howitzer, weighing 45.3 metric tons with 450 mm wide tracks with "parade" pads. Soil moisture at the time of surface treatment is summarized in Table 2.

Table 1.--Summary of the experimental treatments applied at the Dugway Proving Ground.

	<u>TREATMENTS</u>	<u>DRY</u>	vs.	<u>WET</u>
1.	Untreated Control	X		X
2.	1 pass by M110 Howitzer	X		X
3.	4 passes by M110 Howitzer	X		X
4.	10 passes by M110 Howitzer	X		X
5.	Scalped (cryptograms removed)	X		X
6.	Scalped plus 1 pass	X		X
7.	Scalped plus 4 passes	X		X
8.	Scalped plus 10 passes	X		X
9.	Deep raked to disturb vesicular horizon	X		
10.	Scalped plus deep raking	X		
11.	Shallow raking to disturb cryptogams only	X		

Table 2.--Mean soil moisture (%) from grab samples (0-5 cm depth) at the time of soil surface disturbance, 3 July 1991.

<u>Disturbance treatments</u>	<u>Dry</u>	<u>Wet</u>
1 pass by M110 Howitzer	0.71 (0.18) ¹	15.40 (2.86)
4 passes by M110 Howitzer	0.65 (0.04)	14.11 (1.93)
10 passes by M110 Howitzer	0.65 (0.08)	16.56 (0.59)
Scalped	0.72 (0.15)	
Scalped plus 1 pass	0.69 (0.33)	14.07 (3.54)
Scalped plus 4 passes	0.79 (0.11)	13.09 (2.27)
Scalped plus 10 passes	0.75 (0.05)	14.82 (1.22)
Deep raked	0.80 (0.16)	
Scalped plus deep raking	0.69 (0.10)	
Shallow raked	0.71 (0.10)	

¹ Sample standard deviation in parentheses.

Rainfall Simulation

Changes to soil surface characteristics as indexed by infiltration capacity, time to runoff, and interrill erosion were evaluated using a modular drop-forming rainfall simulator as described by Chow and Harbough (1965) and modified by Meeuwig (1971) and Malekuti and Gifford (1978). Infiltration capacity is defined as the maximum possible infiltration rate, said to be a limiting property of the site and influenced by management practices (Brooks et al. 1991, Hawkins and Cundy 1987). Time to runoff is the first flow of water from the runoff plots into the collection troughs. Time to runoff data is presented as a function of the time from rainfall initiation (Dobrowolski et al. 1992). Interrill erosion is indexed by sediment transported from runoff plots (Blackburn 1975).

Runoff plots were defined by driving 0.42 m² steel frames into the soil 7-8 cm deep. Slopes of the runoff plots were approximately 2-4%. The simulator was positioned at a height of 2.2 m, dispensing a raindrop with a mean diameter of 2.8 mm. Based on data reported by Laws (1941), the kinetic energy associated with this drop size and fall distance is approximately 40% of natural rainfall. The simulated rainfall was applied at an intensity of 101.6 mm h⁻¹ for 45 minutes to each air-dry runoff plot within a 10-day period during two summers. This rainfall intensity represents a storm return interval that exceeds 100 years in this area (Hershfield 1961).

Runoff occurred from all plots in this study. Runoff from each plot was pumped into tared containers and weighed at five-minute intervals throughout the rainfall event. Weights

were converted to volume and accumulated over the rainfall simulation event. Infiltration capacities (mm h^{-1}) were determined by calculating the difference between applied rainfall rates and measured runoff rates for that five-minute interval.

Upon termination of the simulated rainfall applications, runoff collections from each plot were thoroughly agitated and 1-liter subsample collected. The sediment was filtered from each subsample, dried at 105°C for 24 h, weighed, and the concentrations used as an index to interrill erosion.

Estimates of cover on the runoff plots were made using a 75 X 75 cm frame divided into 0.14 m^2 areas prior to rainfall application. For each runoff plot the cover (percent) of bare soil and whether or not it was visibly crusted, rock, litter, and microphytic crust was determined using 9 cover classes that totalled 100 percent (Greg-Smith 1964). Surface roughness was indexed using a drop-point frame method adapted from McCool et al. (1976). The point frame, with 1.5 cm spacing was positioned once across the runoff plot. Vertical displacement of the pins was numerically recorded on a scale positioned immediately behind the pins. The standard deviation of the pin displacement was used to represent surface roughness.

Antecedent soil moisture and soil bulk density were determined immediately prior to rainfall simulation at 50 and 100 mm depths adjacent to runoff plots by gravimetric (Gardner 1986) and core (Blake and Hartge 1986) methods, respectively. A composite soil sample of the surface 50 mm was collected within each plot after rainfall simulation, air-dried, passed through a 2 mm sieve, and analyzed for particle size distribution by the hydrometer method (Gee and

Bauder 1986). This sample was also analyzed for aggregate stability by wet sieving (Kemper and Rosenau 1986) and percentage of organic matter by the Walkely-Black method (Nelson and Sommers 1982).

Wind Simulation

A portable wind tunnel described by Gillette (1978) and Gillette et al. (1980, 1982) was used with an open-floored test section so that a variable-speed turbulent boundary layer could be formed over a flat soil that contains small-scale roughness elements. The wind tunnel used a two-dimensional 5:1 contraction section with a honeycomb flow straightener and a roughly conical diffuser attached to the plexiglass working section after Wooding (1968). Cross-sectional dimensions of the working section are 15.24 x 15.24 cm and the length is 240 cm.

Wind velocity data were collected at several heights above the soil surface midway across the end of the working section. The Pitot tube anemometer was calibrated by using the National Center for Atmospheric Research wind tunnel anemometer calibration facility and was corrected for temperature and pressure changes (Gillette, personal communication). The mean velocity u versus height z data were fitted to the function for aerodynamically rough flow (see Priestley 1959, Gillette et al. 1980):

$$u = \frac{u_*}{k} \ln \left(\frac{z}{z_0} \right)$$

where u_* is friction velocity, z_0 is roughness height characteristic of the surface, and k is Von Kármán's constant using a nonlinear least squares routine. The threshold velocity profile was

obtained for the wind velocity at which continuous movement of grains was first visible. Threshold velocities and aerodynamic roughness heights are reported in terms of the friction velocity and roughness height. Threshold friction velocity u_{*t} will hereafter be called the threshold velocity. The wind simulator is capable of simulating a range of wind speeds up to 97 kph.

Detached sediment was collected in two downwind traps constructed of fine and coarse mesh spun fiberglass. Filters were dried at 105°C for 24 h, weighed, and the weight difference converted to kg/ha. Responses recorded were the wind velocity to initiate detachment of mineral soil and organic matter, and the total sediment collected during the wind simulation event which lasts approximately 10 minutes.

Analysis

Data produced from the experiment were analyzed as a 3 X 11 X 2 factorial experiment in a randomized complete block analysis of variance. Rejection of the null hypothesis will be at $\alpha = 0.05$. Mean square error (MSE) residuals were tested for normality and the data were transformed when necessary. Treatment means were separated using Fisher's protected least significant difference multiple range test for equal cell sizes (Box et al. 1978). Simple linear correlation analysis determined the degree of association between dependent variable (infiltration capacity, time to runoff, interrill erosion, and threshold velocity) and regressor variables (soil and vegetation characteristics). Correlations were considered significant at $p \leq 0.05$. Forward stepwise multiple regression (entry and stay level $p \leq 0.05$ and $p < 0.15$,

respectively) was used to identify the most important set of variables influencing infiltration capacity, time to runoff, interrill erosion, and threshold velocity (Draper and Smith 1981).

RESULTS AND DISCUSSION

Surface Characteristics

Significantly greater mineral soil (70-100 percent) was exposed by deep raking, scalping plus raking, scalping and tracked vehicle, or at least four passes of a tracked vehicle when compared to undisturbed, shallow raked, simply scalping the surface, and one pass by a tracked vehicle (Fig. 3). These latter disturbances, though less intense, resulted in significantly greater exposed mineral soil when compared with untreated control plots. One year after treatment, plots that were shallow raked, scalped only, and one pass of the tracked vehicle contained less exposed mineral soil than immediately after the disturbance treatment. All other plots retained the same level of exposed mineral soil.

One pass by a tracked vehicle and shallow raking appeared to either retain litter or contained greater pre-treatment amounts when compared to control plots (Fig. 4). Since woody plants were removed from each treatment at the soil surface, debris from the disturbance was not a prominent source of litter. Litter cover on other treatments was not different than untreated controls.

Vascular plant cover was nonexistent on the plots in 1991 (Fig. 5). In 1992, plant cover increased on all plots, reflecting year to year variation in precipitation. Results showed no apparent differences in vascular plant cover.

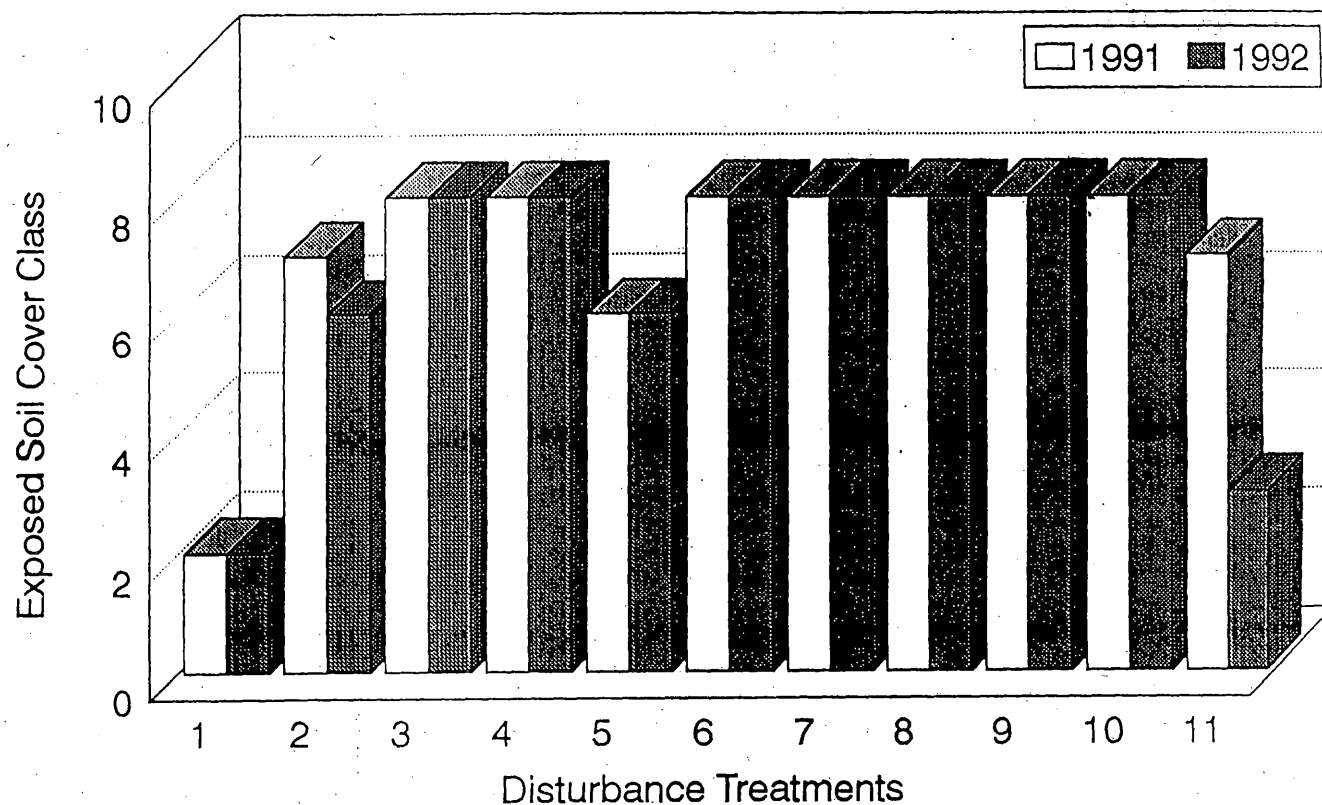


Fig. 3--Mean exposed mineral soil expressed as a member of nine cover classes, 0, Trace = 0.5%, 1 = 1-5%, 2 = 5-10% 3 = 10-25%, 4 = 25-40%, 5 = 40-55%, 6 = 55-70%, 7 = 70-85%, 8 = 85-100. Each bar represents six surface disturbance plots at the Dugway Proving Ground. Treatment legend is found in Table 1, page 9.

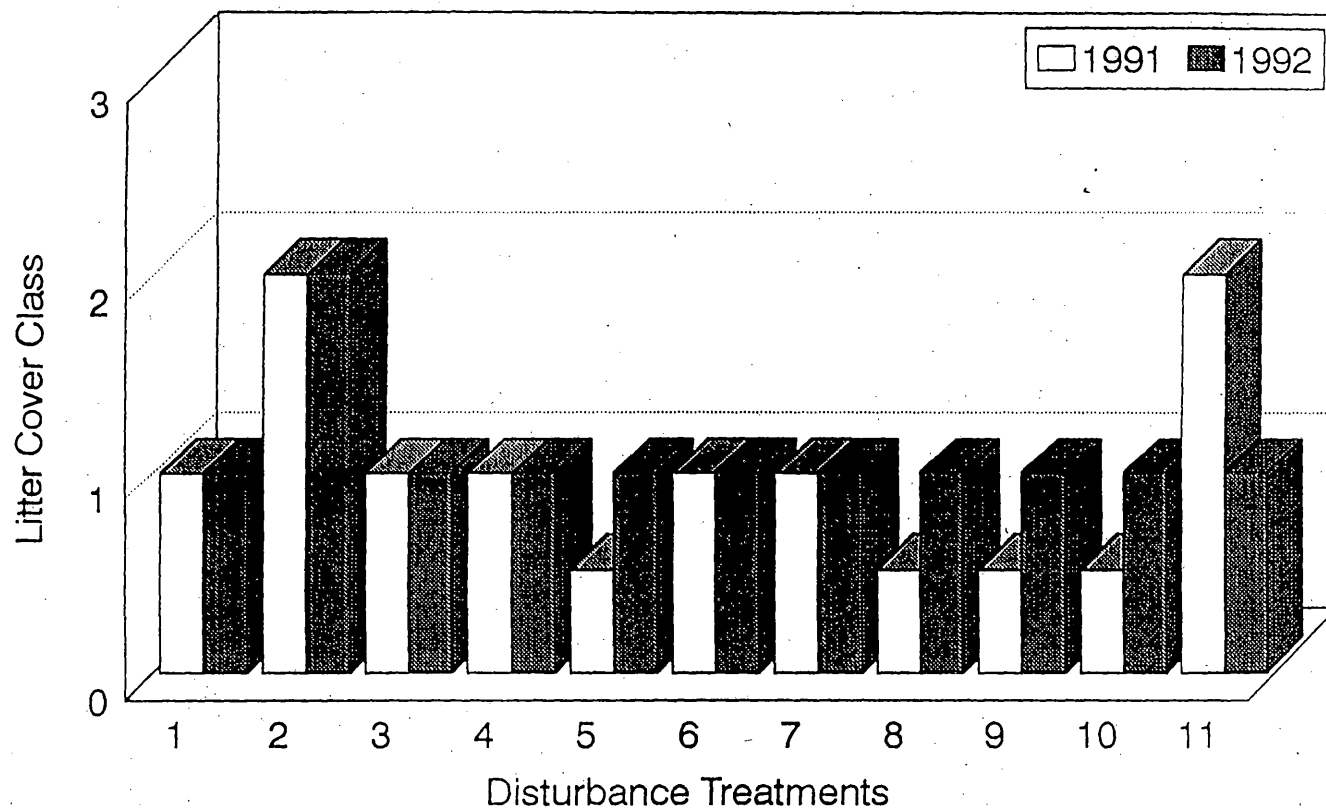


Fig. 4--Mean surface litter expressed as a member of nine cover classes, 0, Trace = 0.5%, 1 = 1-5%, 2 = 5-10% 3 = 10-25%, 4 = 25-40%, 5 = 40-55%, 6 = 55-70%, 7 = 70-85%, 8 = 85-100. Each bar represents six surface disturbance plots at the Dugway Proving Ground. Treatment legend is found in Table 1, page 9.

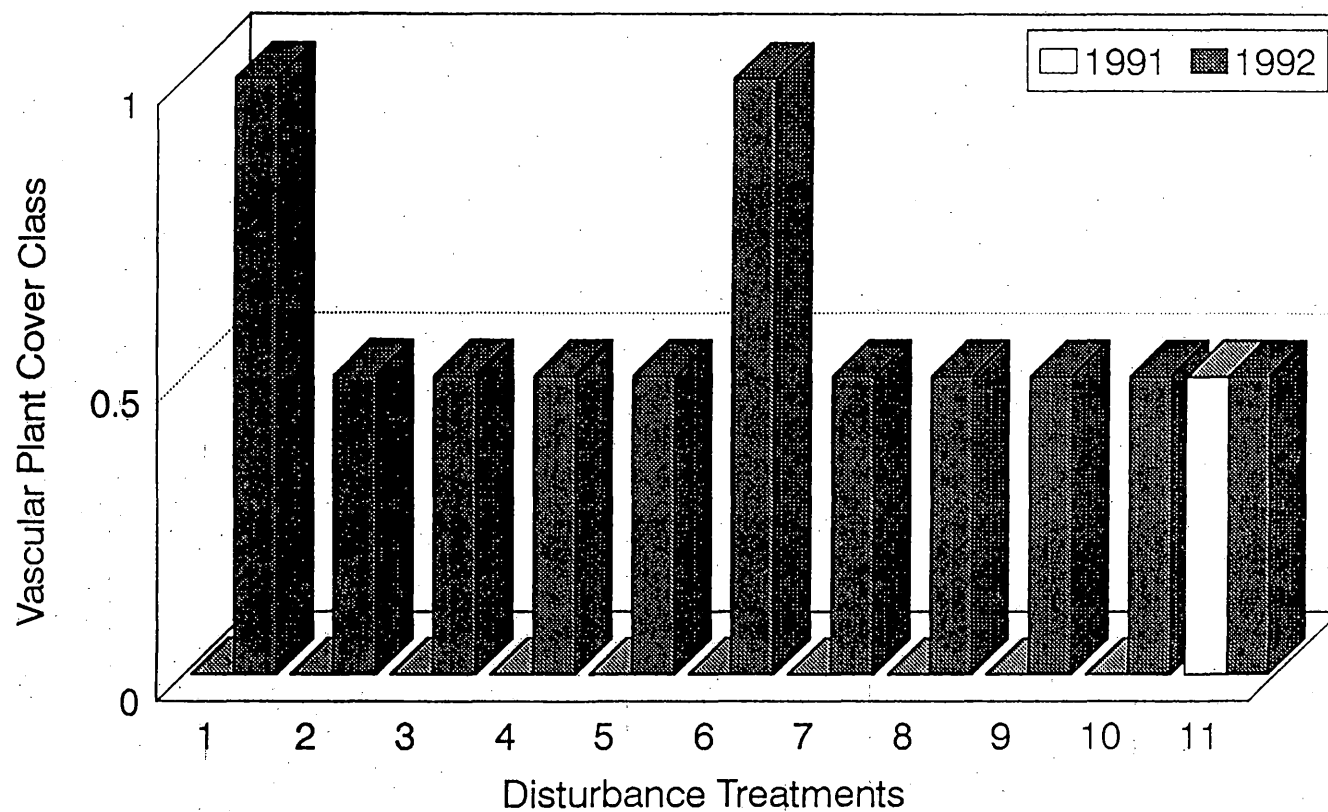


Fig. 5--Mean vascular plants expressed as a member of nine cover classes, O, Trace = 0.5%, 1 = 1-5%, 2 = 5-10%, 3 = 10-25%, 4 = 25-40%, 5 = 40-55%, 6 = 55-70%, 7 = 70-85%, 8 = 85-100. Each bar represents six surface disturbance plots at the Dugway Proving Ground. Treatment legend is found in Table 1, page 9.

All disturbance treatments resulted in significantly lower microphytic crust cover than undisturbed control plots (Fig. 6). Scalping plus an intense disturbance by a tracked vehicle (ten passes) resulted in the lowest cover of microphytes. Other treatments involving the combination of scalping and tracked vehicle disturbance or at least four passes of the tracked vehicle resulted in a significant reduction in microphytic crust and increase in exposed mineral soil. Single disturbance events that result in portions of the intact microphytic crust persisting, appear to retain greater microphytic crust cover and increase that cover within one year (e.g., shallow raked changed from cover class three to six from 1991 to 1992).

Disturbance due to tracked vehicles was observed to influence surface roughness as indexed by the standard deviation of pin-frame values. Significantly greater roughness was found for scalping plus ten passes of the tracked vehicle than all other treatments (Fig. 7). Ten passes of the tracked vehicle produced greater surface roughness than shallow raked and undisturbed control plots. No other treatment differences were detected. Surface roughness sampling in 1991 occurred after a significant rain event that may have assisted in smoothing the surface by raindrop impact. Roughness significantly declined by 1992 for all treatments with the exception of shallow raking. This decline in roughness may reflect the smoothing action of freeze-thaw cycling, raindrop impact, and/or erosion.

Soil Characteristics

Particle size analysis indicated no detectable differences in percent sand and silt between treatments (Figs. 8 and 9). Clay-sized particles appeared to be slightly higher on some scalped

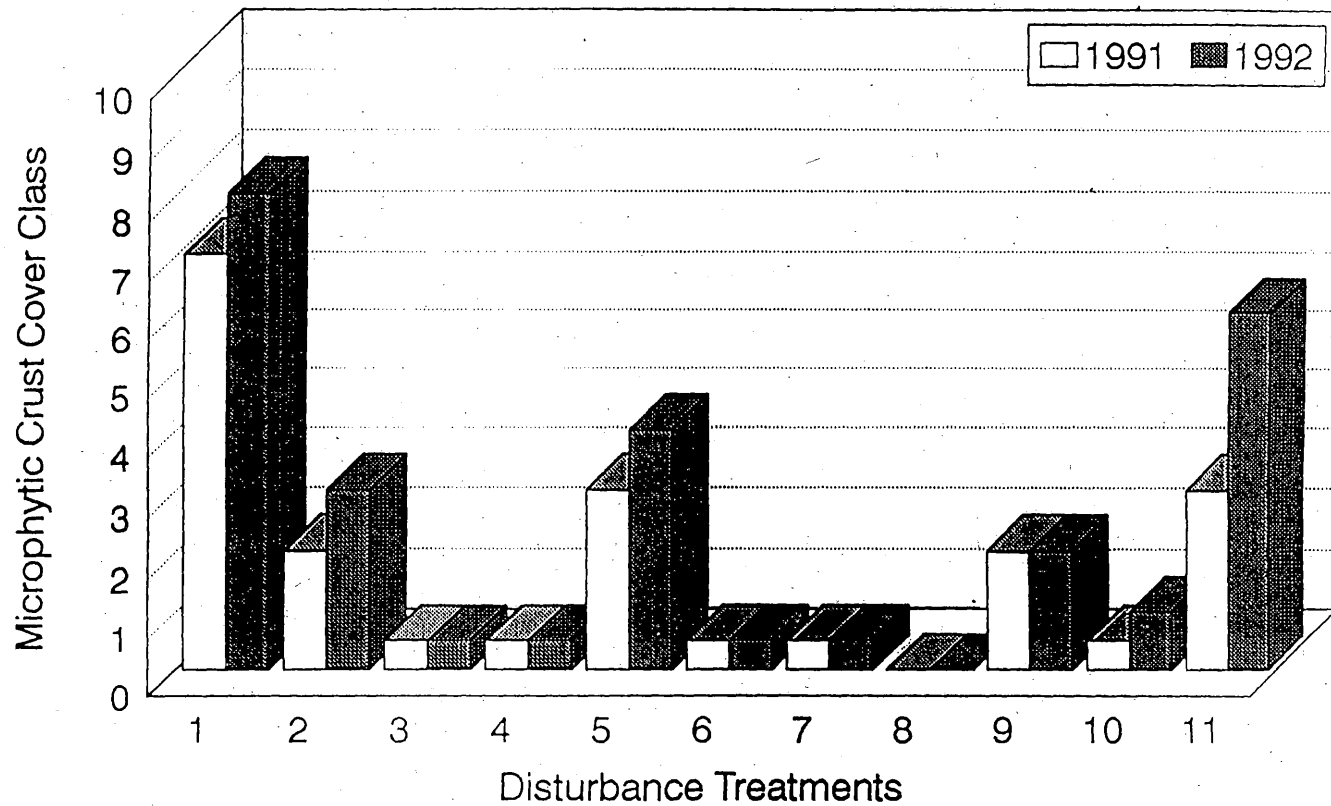


Fig. 6--Mean microphytic crust expressed as a member of nine cover classes, O, Trace = 0.5%, 1 = 1-5%, 2 = 5-10%, 3 = 10-25%, 4 = 25-40%, 5 = 40-55%, 6 = 55-70%, 7 = 70-85%, 8 = 85-100. Each bar represents six surface disturbance plots at the Dugway Proving Ground. Treatment legend is found in Table 1, page 9.

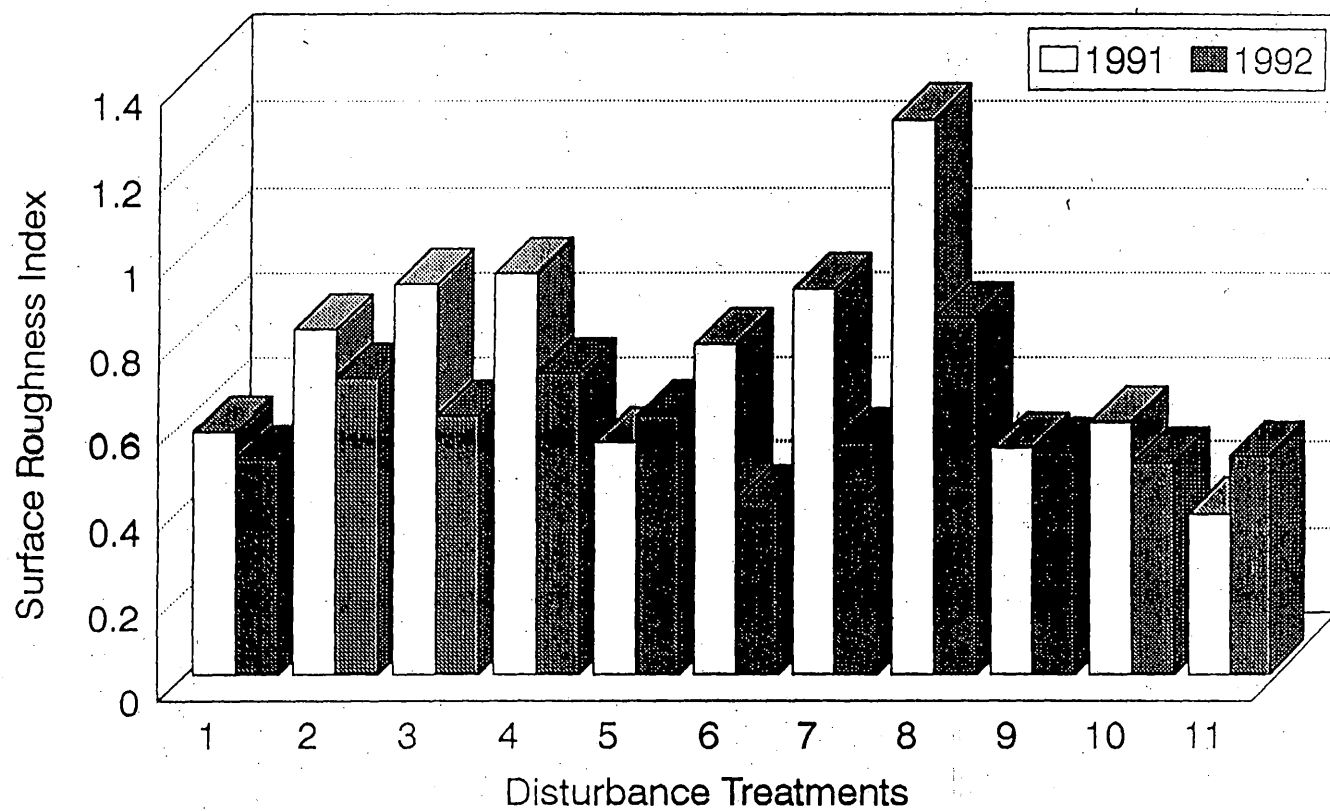


Fig. 7--Mean values of the surface roughness index for eleven disturbance treatments ($n = 6$) at the Dugway Proving Ground. The treatment legend is in Table 1, page 9.

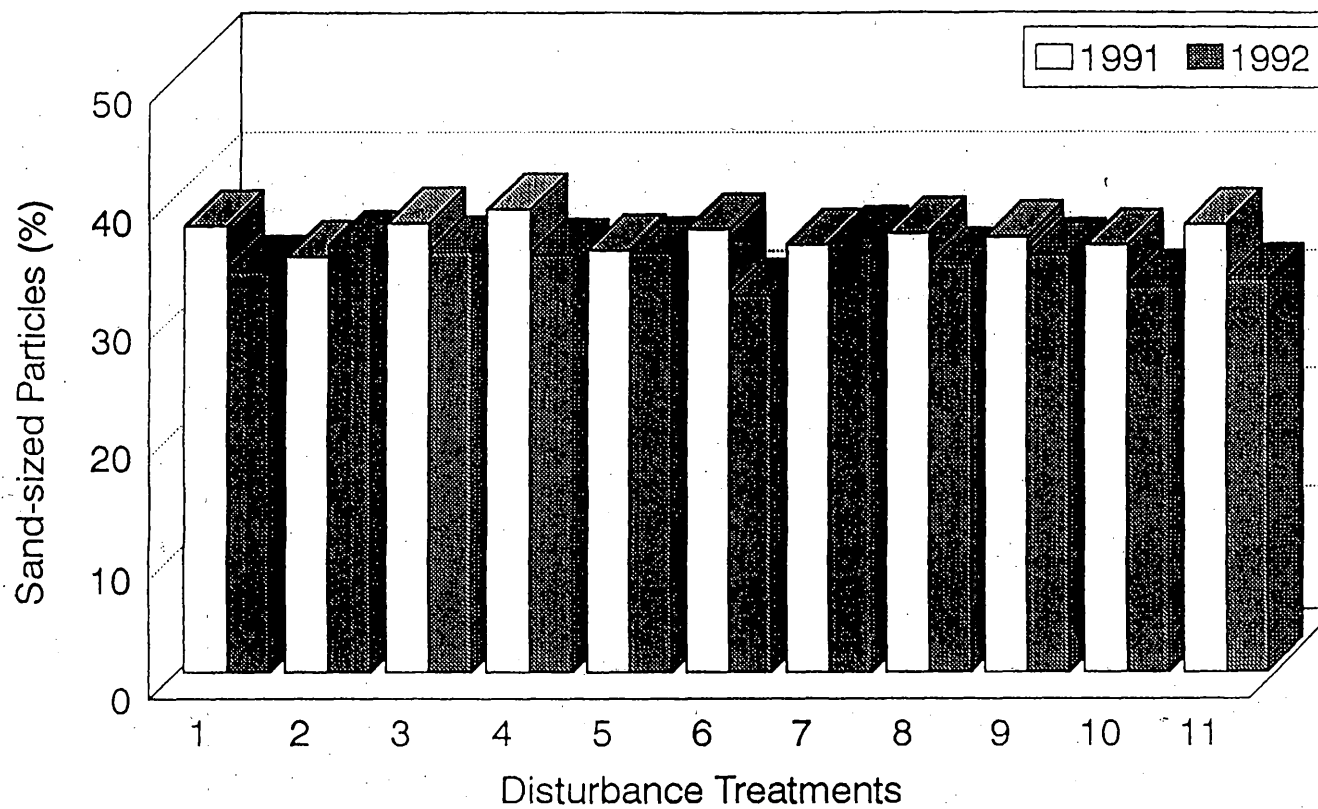


Fig. 8--Mean sand-sized particles (%) in each disturbance plot surface at the Dugway Proving Ground. Treatment legend is found in Table 1, page 9.

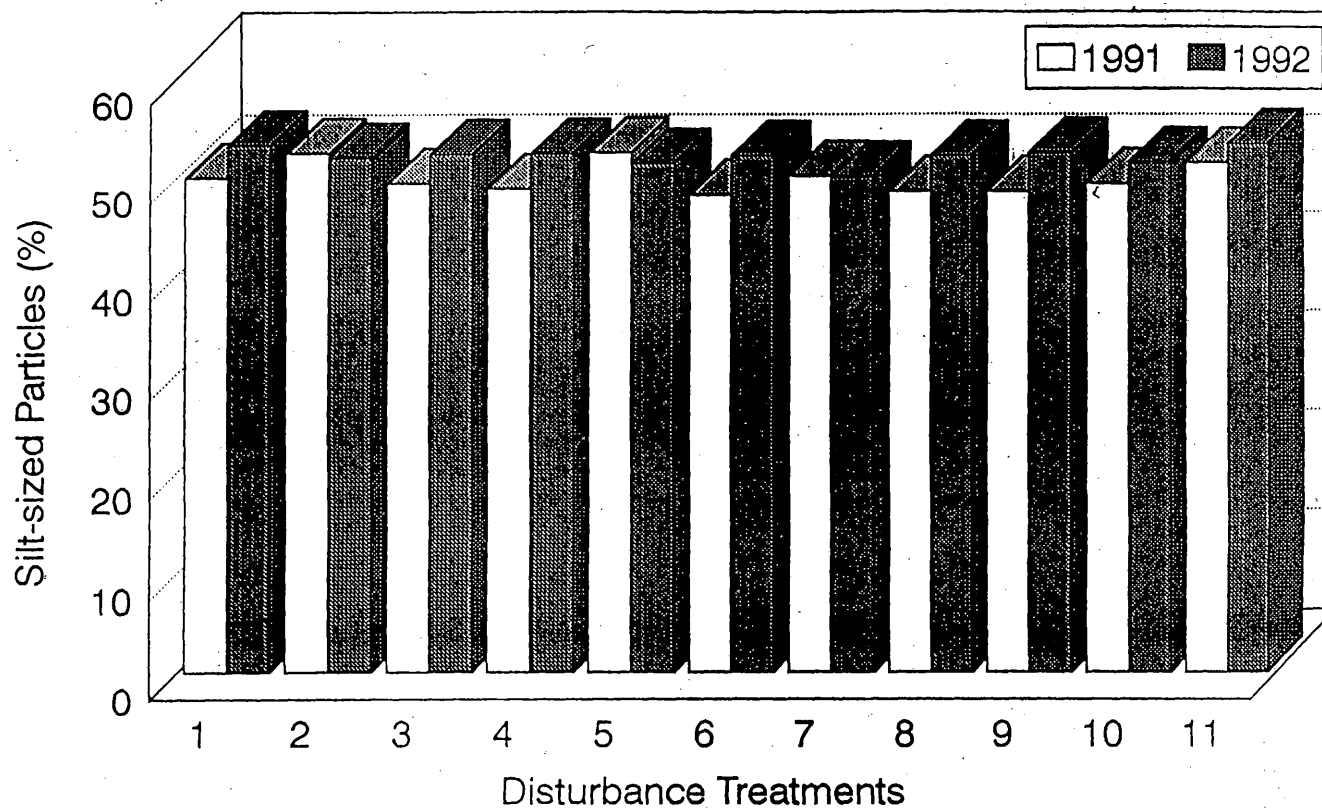


Fig. 9--Mean silt-sized particles (%) in each disturbance plot surface at the Dugway Proving Ground. Treatment legend is found in Table 1, page 9.

plots, possibly reflecting differences between replications (Fig. 10). Aggregate stability and organic matter were not significantly different between treatments based upon the data obtained from this study (Figs. 11 and 12). No detectable treatment differences in bulk density at the 0-5 and 5-10 cm were found (Figs. 13 and 14). The lack of significant treatment differences is expected, all plots were placed within a 100 m radius of each other. Although great spatial and temporal variability exist between shrub coppice dunes and dune interspaces, interspace characteristics may be similar (Eckert et al. 1986).

Antecedent soil moisture at 0-5 and 5-10 cm depths exhibit significant differences between treatments, however these differences are difficult to interpret. No intuitively pleasing explanation is easily produced to explain the differences. Spatial variability in antecedent soil moisture is often important in rainfall simulation studies (Dobrowolski et al. 1992), in some cases masking treatment effects. The differences indicated by Figs. 15 and 16 may be statistically significant, but ecologically irrelevant.

Infiltration Capacities and Time to Runoff

Mean infiltration capacities after 45 minutes often displays the greatest correlation with other variables and it is the most consistently stable portion of the infiltration capacity curve (Dobrowolski et al. 1992). Thus, infiltration capacity after 45 minutes is the only infiltration variable considered in the following discussion. Mean infiltration capacity after 45 minutes was significantly lower for all disturbance treatments when compared to the undisturbed control except scalping alone and shallow raking (Fig. 17). Ten passes alone and scalping plus ten

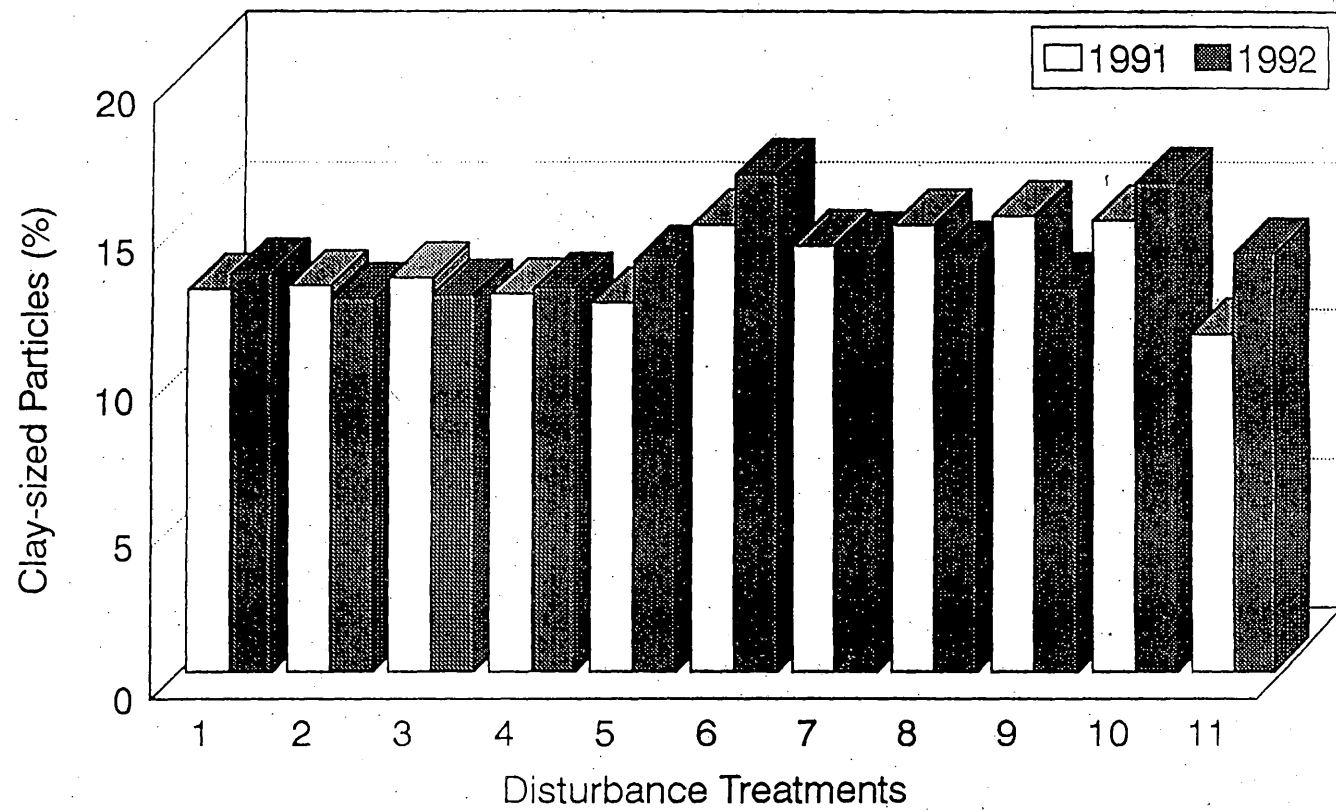


Fig. 10--Mean clay-sized particles (%) in each disturbance plot surface at the Dugway Proving Ground. Treatment legend is found in Table 1, page 9.

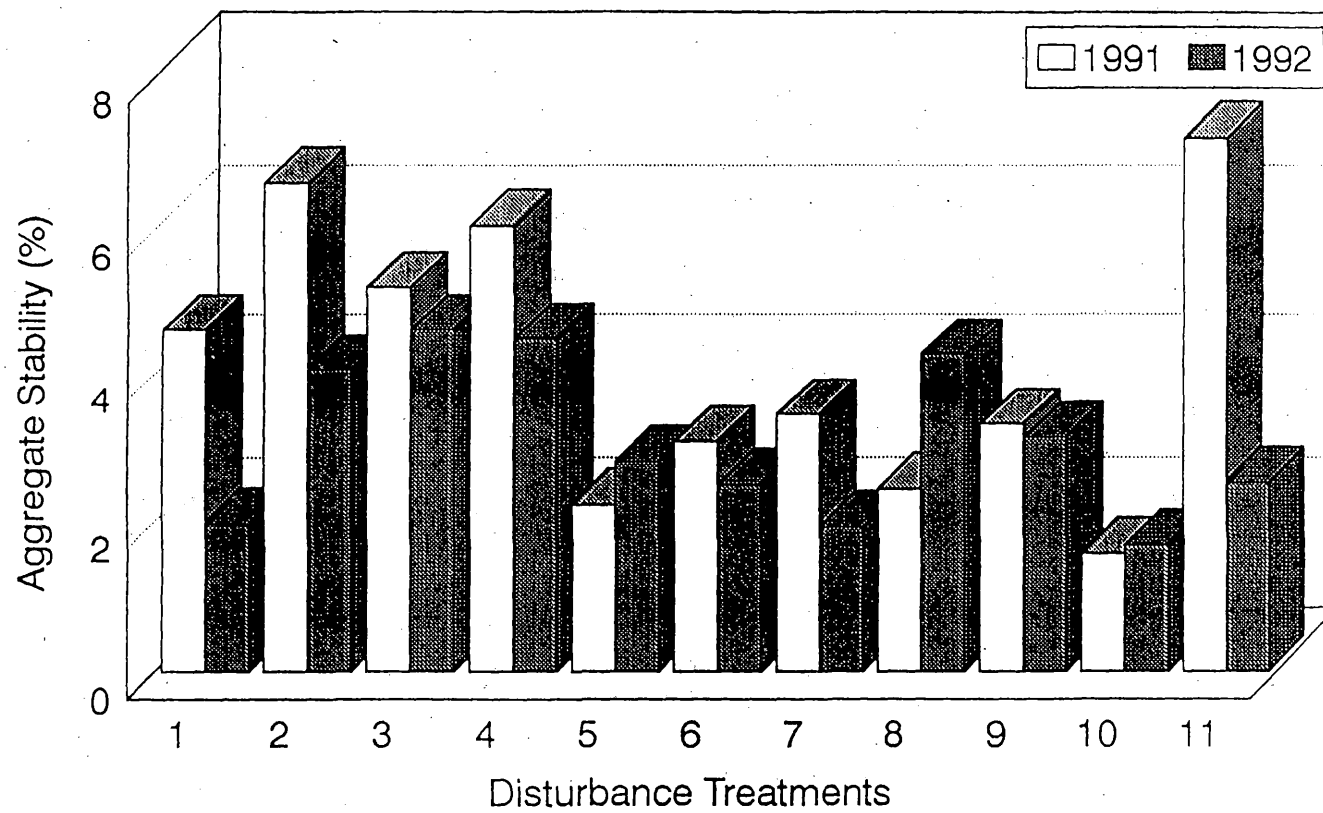


Fig. 11--Mean aggregate stability (%) for surface disturbance treatments (n=6) at the Dugway Proving Ground. Treatment legend is found in Table 1, page 9.

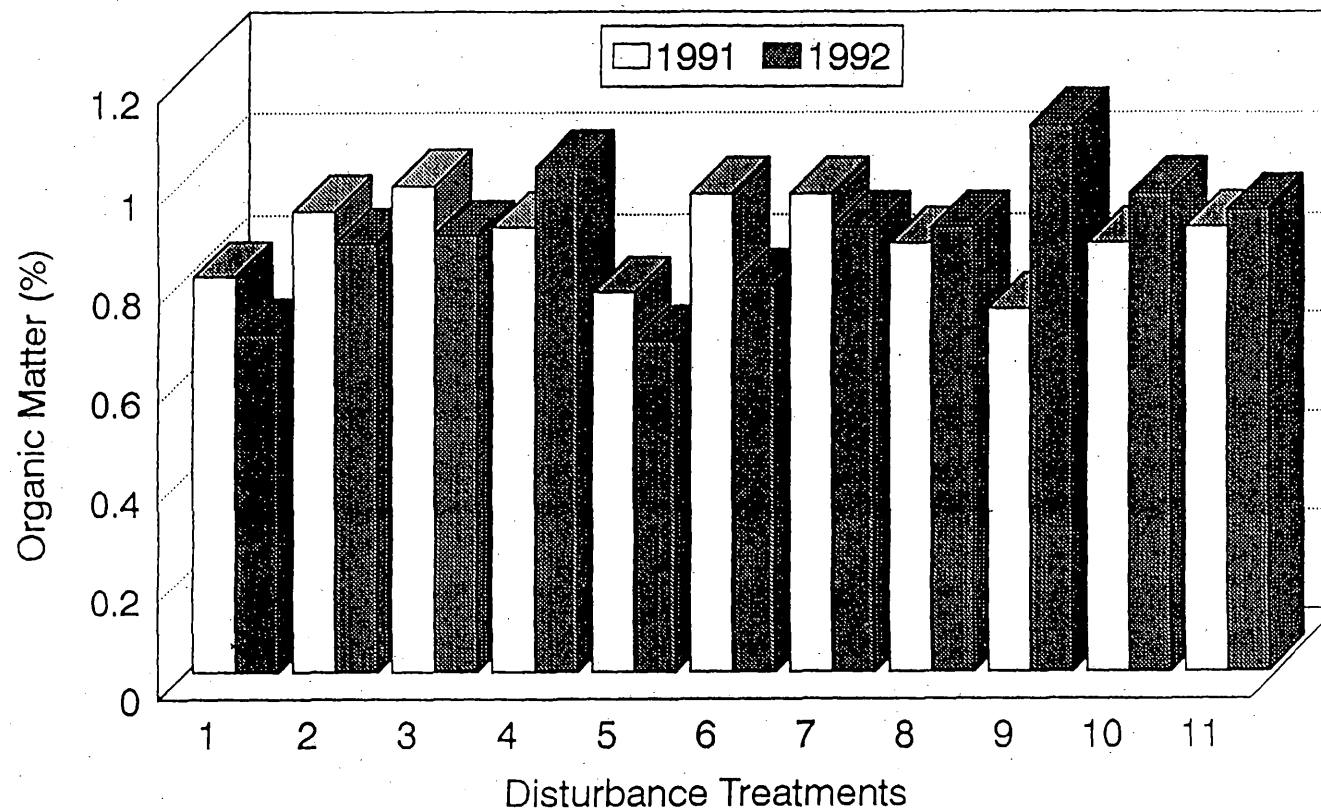


Fig. 12--Mean organic matter (%) for surface disturbance treatments (n=6) at the Dugway Proving Ground. Treatment legend is found in Table 1, page 9.

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This figure will be added in the amended report.

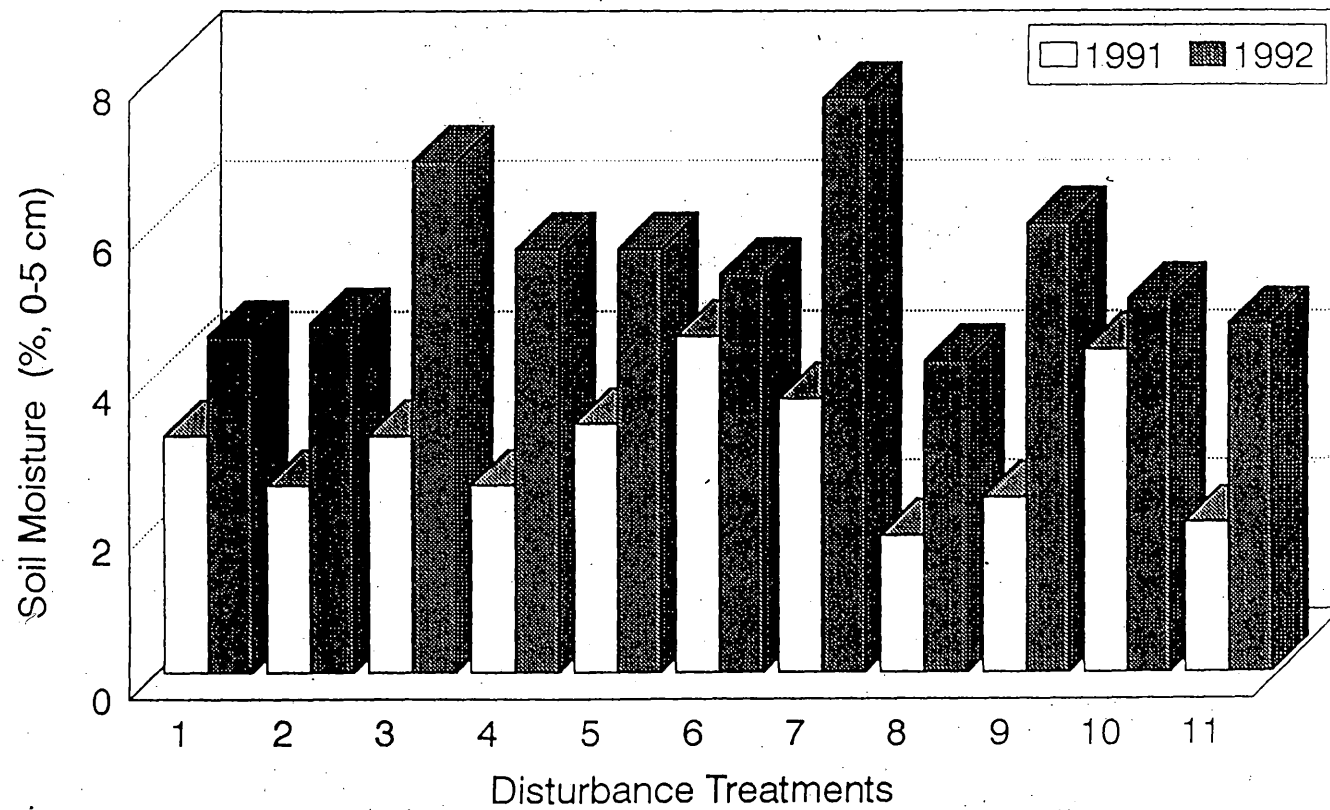


Fig. 15--Mean antecedent soil moisture (0-5 cm depth, %) for surface disturbance treatments (n=6) at the Dugway Proving Ground. Treatment legend is found in Table 1, page 9.

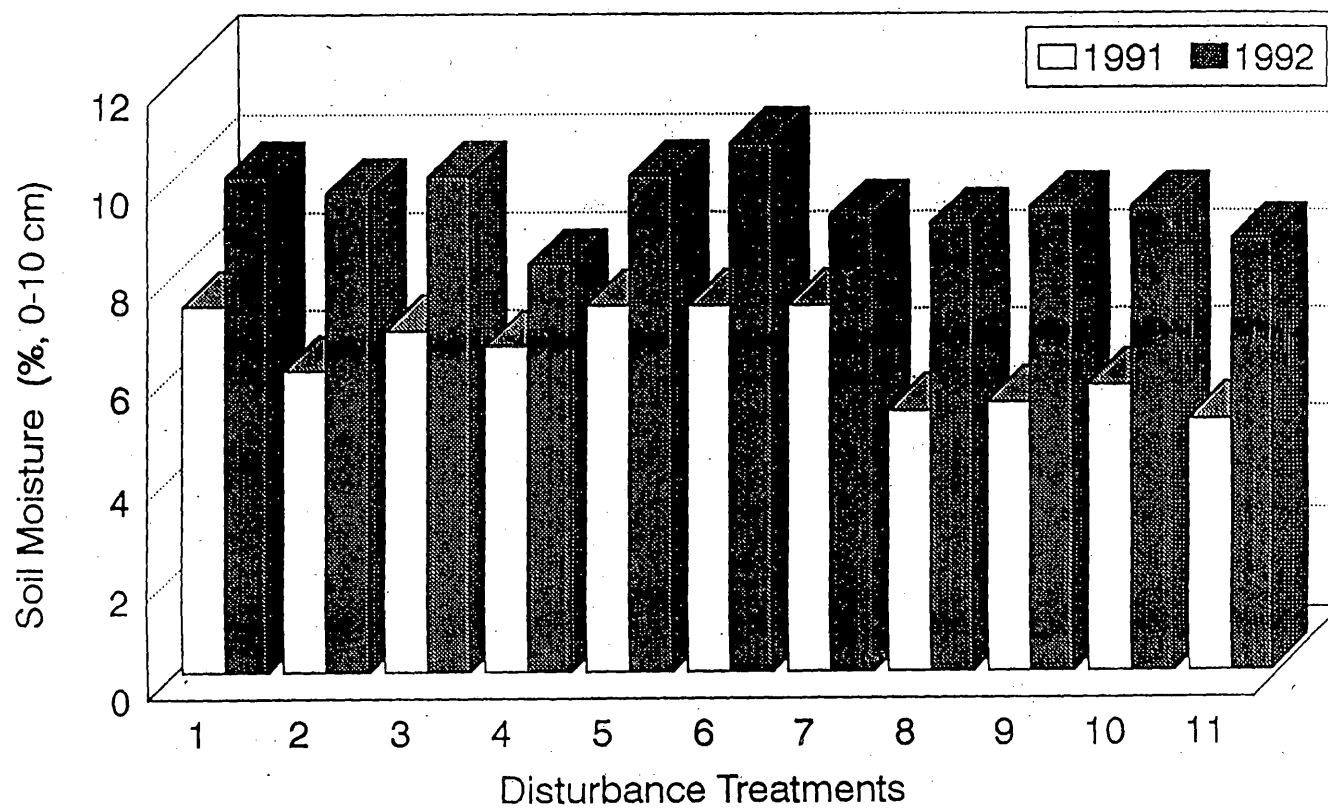


Fig. 16--Mean antecedent soil moisture (5-10 cm depth, %) for surface disturbance treatments (n=6) at the Dugway Proving Ground. Treatment legend is found in Table 1, page 9.

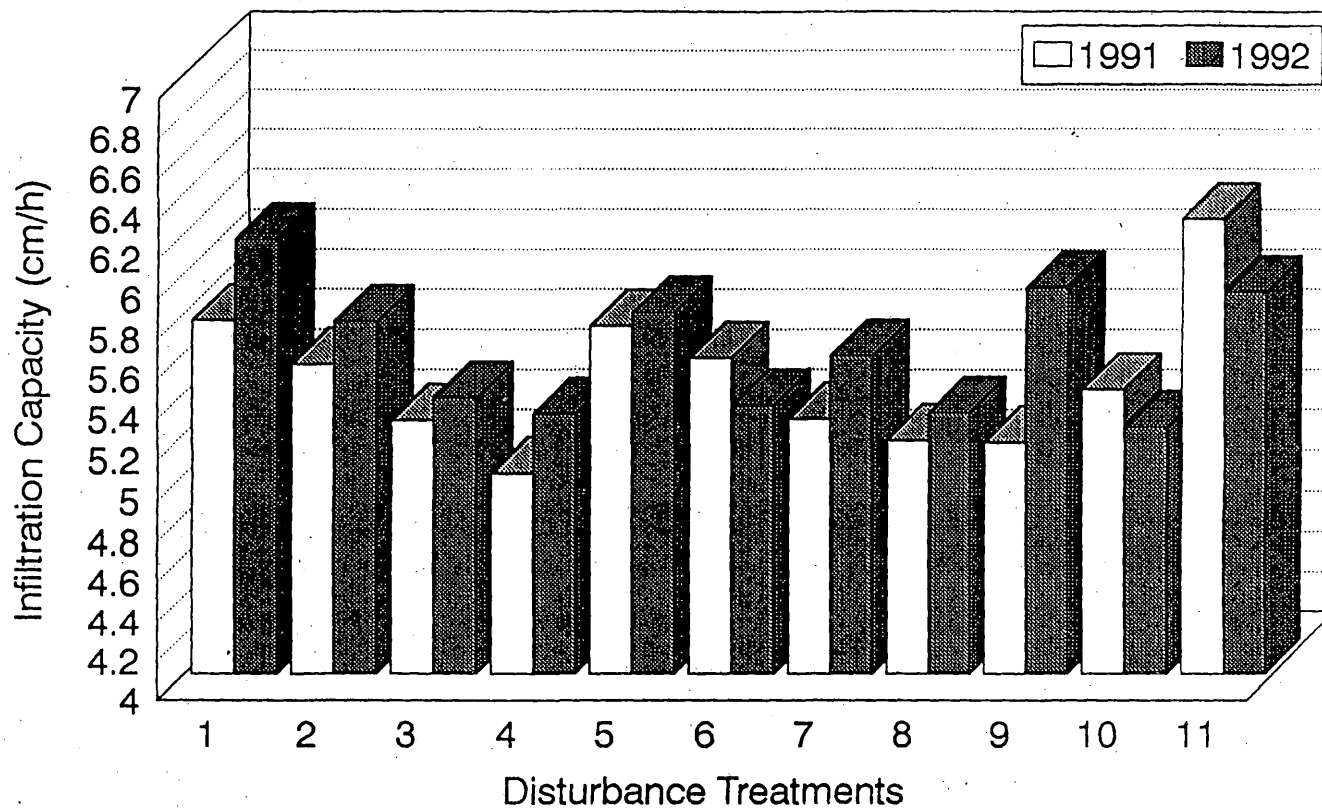


Fig. 17--Mean infiltration capacity (cm/h) for disturbance treatment plots at the Dugway Proving Ground. Legend for the disturbance treatments is found in Table 1, page 9.

passes produced the lowest infiltration capacities. These disturbances represented the most severe treatments and may have initially reduced the influence of the vesicular horizon. Prior to rainfall simulation, however, the soil underwent wetting and drying potentially reconstituting the vesicular horizon. In addition, the reduction of surface cover and exposure of the plot to direct raindrop impact, slaking and transient surface sealing. Other disturbance treatments resulted in better infiltration characteristics than the severe ten pass treatment, though significantly reducing infiltration capacity after 45 minutes of simulated rainfall. Multiple disturbance events appear to reduce infiltration capacity to a greater degree than single disturbance events. Improvement of infiltration capacity after 45 minutes in 1992 was not consistent for all treatments. Deep raking, intended to disturb the vesicular horizon and thereby potentially improve infiltration capacity, contrastingly reduced infiltration capacity relative to shallow raking and the undisturbed control. Scalped plus deep raked treatments reduced infiltration rate even further.

Time to runoff followed the same relationship as infiltration capacity after 45 minutes (Fig 18). Significantly shorter time to runoff was associated with ten passes and scalping plus ten passes. All disturbance treatments had significantly shorter time to runoff when compared to the control plot with the exception of shallow raking. As the number of repeated disturbances on the same plot increased, time to runoff declined. Further restriction of variability using analysis of covariance provided little additional insight into infiltration capacity or time to runoff. Stepwise regression analysis was used to identify the set of measured

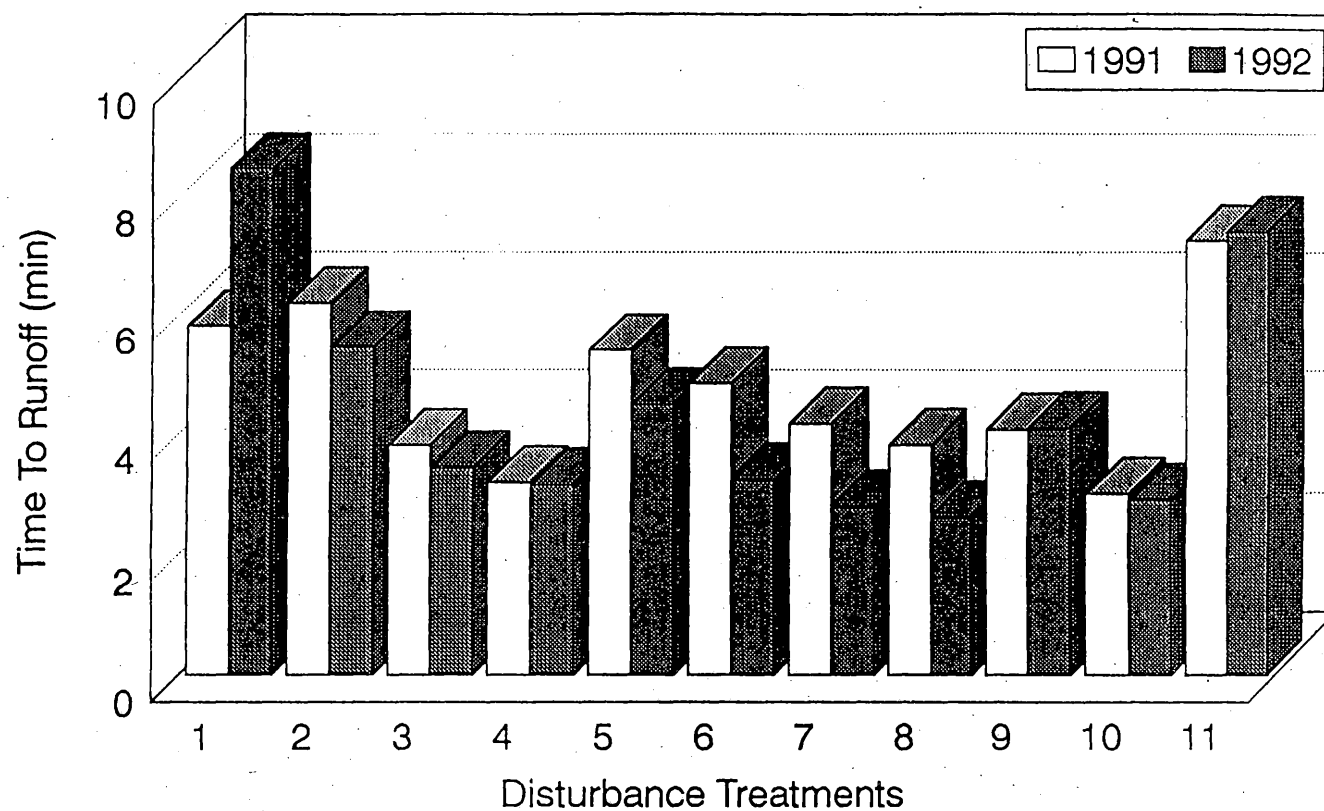


Fig. 18--Mean time to runoff (min) for disturbance treatment plots at the Dugway Proving Ground. Legend for the disturbance treatments if ound in Table 1, page 9.

variables that most effectively predicted infiltration capacity after 45 minutes and time to runoff for both sampling periods (Table 3). The predictive capability was not increased when additional variables were included. Infiltration capacity evaluations reflected the influence of surface characteristics disturbed by the treatment perturbations. Simple linear correlation revealed that infiltration capacity after disturbance was directly related to microphytic crust cover ($r = 0.57$), with a weaker relationship to litter ($r = 0.23$). A negative relationship existed between exposed mineral soil ($r = -0.53$), surface roughness ($r = -0.28$) and infiltration capacity. Although soil moisture at the 0-5 cm depth entered the stepwise regression, no relationship appears to exist with infiltration capacity ($r = -0.09$). Exposed mineral soil may slake when submitted to direct raindrop impact, forming a transient seal and concomitantly reducing infiltration capacities. Visual evidence of surface sealing was evident on rainfall simulation plots prior to and during rain events. Surface covers such as litter and microphytic crust tend to intercept rain and may lessen the effects of raindrop impact in slaking and sealing processes.

Surface characteristics influenced time to runoff after disturbance. Time to runoff was highly correlated with infiltration capacity after 45 minute ($r = 0.70$), resulting in similar relationships with surface characteristics.

From our study, it does appear that repeated disturbance by tracked vehicles degrades infiltration capacities and decreases time to runoff, and the effects of these disturbances are not ameliorated within one year. Disturbing the vesicular horizon by deep raking does not appear to improve infiltration characteristics or increase time to runoff when compared to the

Table 3--Predictive equations for the response variables infiltration capacity after 45 minutes (IC45), time to runoff (TRO), and sediment concentration (SED) produced from stepwise regression for the surface disturbance treatments, Dugway Proving Ground. All equations are significant at $p \leq 0.15$ and $n = 108$.

Regression Equation	Coefficient of Determination (R^2)
IC45 (cm/h) = 4.54 + 0.07 (exposed soil, standard error 0.07) + 0.13 (litter, s.e. 0.05) + 0.15 (microphytic crust, s.e. 0.05) - 0.11 (surface roughness, s.e. 0.10) + 1.87 (soil moisture 0-5 cm, %, s.e. 1.73)	0.38
TRO (min) = 4.14 + 0.51 (litter, s.e. 0.24) + 0.51 (microphytic crust, s.e. 0.06) - 14.89 (soil moisture 0-5, %, s.e. 8.42) +12.91 (soil moisture 5-10, %, s.e. 8.77) - 1.19 (bulk density, g/cm ³ , s.e. 0.66)	0.51
SED (g/l) = 24.37 - 0.68 (exposed soil, s.e. 0.72) - 1.79 (microphytic crust, s.e. 0.57) - 0.23 (aggregate stability, s.e. 0.14) +0.18 (sand, %, s.e. 0.14) - 55.4 (soil moisture 0-5 cm, %, s.e. 22.11) +34.05 (soil moisture 5-10, %, s.e. 23.43) - 8.41 (bulk density 0-5 cm, %, s.e. 1.77)	0.57

undisturbed control. Removal of the microphytic crust by scalping seems to reduce infiltration capacity, though disturbing the surface by raking while leaving some intact crusts does not seem to degrade infiltration capacity.

Sediment Concentrations

Sediment transported from rainfall simulator plots was significantly greater from ten passes and scalping plus ten passes disturbances when compared to undisturbed controls and shallow raking (Fig. 19). Elevated sediment concentration appeared to be the result of disturbance and exposure of mineral soil to the disaggregating effects of raindrop impact. Under disturbance conditions of less than ten passes, scalping, scalping plus tracked vehicle disturbance, and deep raking, appeared to produce more sediment than one or four passes of the tracked vehicle alone.

Measured variables in stepwise regression analysis that most effectively predicted sediment concentration reflected surface cover and surface soil conditions. Simple linear correlation revealed that sediment concentration was positively related to exposed mineral soil ($r = 0.53$) and the sand particle size fraction ($r = 0.30$). Negative relationships were found for the presence of a microphytic crust cover ($r = -0.55$). The influence of microphytic crust appears to be associated with binding the soil surface together, thereby reducing the disaggregating effects of raindrop impact. Negative relationships were also revealed between sediment concentration and soil moisture at the 0-5 cm ($r = -0.32$) and 5-10 cm ($r = -0.33$). As bulk density at 0-5 cm decreased due to "fluffing" by the passage of vehicle tracks, sediment

concentration increased, as evidenced by the negative relationship between bulk density and sediment concentration ($r = -0.47$).

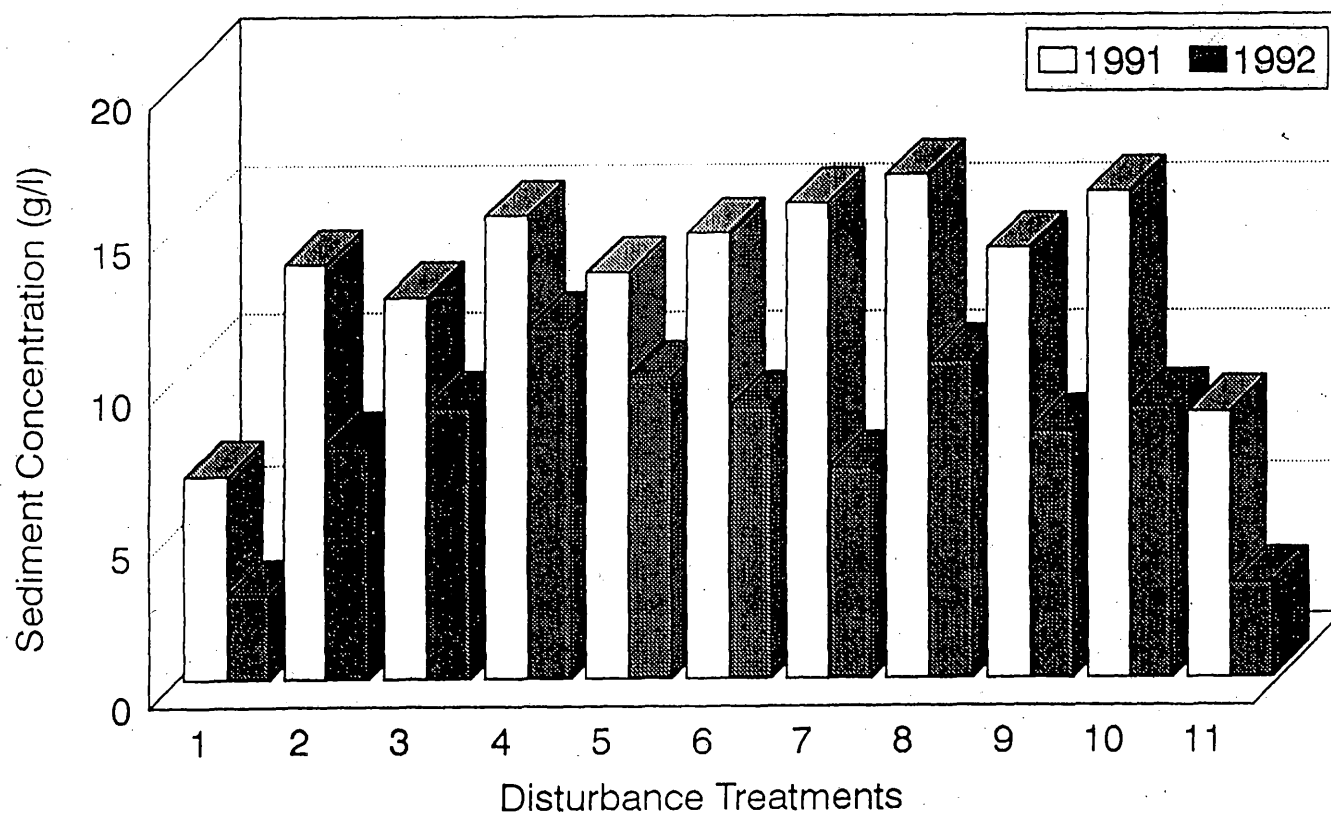


Fig. 19--Mean sediment concentration (g/l) for disturbance treatment plots at the Dugway Proving Ground. Legend for the disturbance treatments is found in Table 1, page 9.

Wind simulation results and discussion

will appear in the amended report.

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United States Department of the Interior



NATIONAL PARK SERVICE

Southeast Utah Group

Arches and Canyonlands National Parks

Natural Bridges National Monument

Moab, Utah 84532-2995

IN REPLY REFER TO:

A44 (SEUG-RM)

December 1, 1992

E. Durant McArthur
Project Leader
Shrub Sciences Lab
735 North 500 East
Provo, Utah 84606

Dear Mr. McArthur:

Enclosed is an interim report for Interagency Agreement INT-92686-IA, Cryptobiotic Crust Biology and Management in Arches and Canyonlands National Parks. A draft manuscript from this project is included as well.

If you have any questions, please contact Jayne Belnap at (801) 259-7164.

Sincerely,

Walter D. Dabney
Superintendent
Southeast Utah Group

Enclosures

INTERIM REPORT: CRYPTOBIOTIC CRUST BIOLOGY AND MANAGEMENT IN
ARCHES AND CANYONLANDS NATIONAL PARKS

Interagency Agreement INT-92686-IA

Jayne Belnap, Research Ecologist, National Park Service

OVERVIEW: As per this agreement, the effect of trampling and off-road traffic was investigated at Dugway Proving Grounds, and Arches and Canyonlands National Parks. Nitrogenase activity and chlorophyll levels of the crusts was examined, as well as the nutrient status of plants growing in disturbed and undisturbed areas. Other aspects of the disturbed systems were measured as well.

Studies at Arches and Canyonlands NP in Spring, 1992 demonstrated that visitor trampling has severely effected grass and shrub ecosystems in these park units. The trampled area studied in Arches is a 5 acre area that 10-15 people walk through daily March to October; it receives very little use during the 4 winter months. This site was compared to a site 500' away that receives very low use. In Canyonlands, a pristine non-trampled grassland was compared to a neighboring grassland that was released from grazing 28 years ago, and currently receives moderate to mid-level use. Experimental tramplings were also done to examine the effects of different types of disturbance.

Upon examination, striking differences between trampled and untrampled areas emerged. A dramatic drop in nitrogen input into the system was seen, with virtually no nitrogenase activity detectable in cyanobacterial populations after a single footprint disrupted the soil crust; this depressed nitrogenase activity was true for the trampled area as a whole when compared with high nitrogenase activity in the less used areas. Nitrogen fixation was disrupted with all types of disturbance tested, including mountain bike tracks, four-wheel drive vehicles and mobile howitzer tracks. At Arches, total nitrogen contents in dominant plants was also much lower in the trampled area: the dominant annual grass, Festuca octoflora (fescue) had 8% lower total nitrogen content in its tissues, while Streptanthella longirostris, the dominant annual forb, had 30% less. The dominant shrub Coleogyne ramosissima (blackbrush) leaves had 8% less nitrogen and seedlings had 5% less nitrogen content. Fescue had an average weight in the trampled area that was 60% less than in the less-trampled area. Mycorrhizae, critical for nutrient and water uptake for many desert plants, had much lower infection rates in blackbrush seedlings from the trampled area than the untrampled area. Both fescue and blackbrush are important wildlife forage: rabbits rely heavily on Festuca, bighorn sheep rely heavily on mature blackbrush, and mice use blackbrush seedlings. Any impact to the physiological functioning or nutritional content of these species is of great concern to managers.

Plant community structure was impacted as well at the Arches

trampled site. Plants were spaced further apart, and there were fewer individuals in the trampled area. There were fewer plants in the interspaces between shrubs, and trampled areas had more annual plant species, or species that act like annuals (in that they have above-ground parts only in the spring), while the untrampled area had more perennial species.

The effect of trampling on soils and soil communities was looked at as well. This included infiltration and compaction of the soils; soil crustal communities; and bacterial and fungal biomass. Again, large effects were noted. Water infiltration rates in trampled areas in Arches were 90% lower than in untrampled areas, resulting in overall water loss to the system. Compaction, affecting invertebrate populations and water retention capabilities of soils, was 5 times greater in the trampled area. Soil crustal communities, important for soil stability, water infiltration, seedling establishment and nutrient status of vascular plants, were disrupted in the trampled areas: in Arches, instead of the rich diversity of lichens and cyanobacteria found in the untrampled area, only one species of cyanobacteria could be found in the disturbed area. Crustal integrity was destroyed in the trampled area as well, whereas the low use area had thick, well-developed crusts.

In the Canyonlands site, bacteria and fungi values were greatly altered by trampling. Both bacteria and fungi showed reduction in total and active biomass in the impacted area when compared to the pristine site. Consequently, plant litter may stay intact much longer in these impacted areas, rather than being decomposed. Nutrients in the litter are then not available to living vascular plants, and the natural nutrient cycle is disrupted. Bacteria to fungi ratios were also higher in the trampled area when compared to the pristine site. Previous research has demonstrated that higher ratios either lead to, or are associated with, a shift from perennial to annual plant communities (which may be correlated with the plant species shift seen at the Arches site).

Sites at Dugway Proving Grounds were assessed as well. This study examined the effects of different surface disturbances (raking, scalping, and tracked vehicles) on nitrogenase activity, chlorophyll content and chlorophyll degradation in these crusts two years after the disturbances. Any disturbance was found to reduce nitrogenase activity by 77-97%, with no significant recovery seen after the two years. Chlorophyll content was significantly lower in the scalped treatments, and not different between any of the others. This demonstrated that recovery of cyanobacterial and green algal biomass is fairly quick unless surface material is removed. No differences were seen in chlorophyll degradation rates between the treatments. Rapid recovery of chlorophyll, and non-recovery of nitrogenase activity demonstrates that the physiological functioning of these crusts may be impaired long after they have recovered their original biomass or visual aspects.

It can be reasonably asserted that the above effects will be true in systems similar to those found in Canyonlands and Arches, consequently placing all desert areas at risk where trampling occurs. Most current management strategy is to disperse use to avoid overuse of resources in any given area. The above evidence indicates that this may not be an appropriate response in these areas, or in any area where soils are highly compactable, systems are dependent on soil crusts for nitrogen and stability, or in areas that receive high levels of use. Since any off-trail activity may be detrimental in significant ways to such ecosystems, management actions need to reflect this. It is critical, therefore, that these studies be expanded and that the severity and extent of the above phenomena be documented quickly. It is imperative that we understand the consequences of this use before system-wide damage occurs.

Nitrogenase Activity in Cryptobiotic Crusts: Effects of Surface Disturbance

INTRODUCTION

Nitrogen levels are known to be low in desert systems relative to other systems. Total atmospheric input over the past 10 000 years has been conservatively estimated to be only 2.99 kg N/m², with 77% of this lost through wind erosion, ammonia volatilization, nitrification, and denitrification (Peterjohn and Schlesinger 1990). Among deserts, cold deserts are expected to have even lower nitrogen levels, as extensive surveys have revealed only a few nitrogen-fixing plants, or rhizosperes, in these regions (Wullstein, 1989; Farnsworth et al. 1976). In addition, concentration of nitrogen around perennial plants, through litterfall and "mining" of the interspace by plant roots, results in interspaces having even lower levels of essential nutrients. Since nitrogen has been shown to limit net primary productivity in many desert ecosystems (Ettershank et al. 1978; Fisher et al. 1988; Nobel et al. 1988; James and Jurinak 1978; Romney et al. 1978), any biological input is critical to the continuing fertility of these cold-desert regions.

Most cold deserts are dominated by cyanobacterial-lichen soil crusts. These crusts often represent 70% or more of the living cover in these areas, and can be up to 10 cm thick. Many rainfall events in desert areas are often not large enough to promote plant growth, but do stimulate microbial community activity. Since cyanobacterial-lichen soil crusts fix both carbon and nitrogen that has been demonstrated to affect the nutrition of nearby vascular plants (Belnap and Harper 1993; Harper and Belnap 1993; Belnap 1992; Mayland et al 1966; Mayland and MacIntosh 1966), they may be able to supply these nutrients to the system on a more continuous temporal basis than many plant species. In addition, their presence in interspaces as well as under vascular plants may play a critical role in maintaining a more homogenous nutrient landscape in deserts.

Most soil crusts in the cold-desert regions of the Colorado Plateau (southern Utah, northern Arizona, and western Colorado) are dominated by the cyanobacteria Microcoleus vaginatus and M. chthonoplastes. Well-developed, undisturbed crusts contain the cyanobacterium Scytonema myochrous and the soil lichen Collema tenax (with the cyanobacterium Nostoc as a phycobiont) as well. Microcoleus vaginatus and M. chthonoplastes are filamentous species that occur as multiple filaments contained within a single, extracellular polysaccharide sheath. These species lack heterocysts, the thick-walled cells where nitrogen fixation generally takes place. S. myochrous and Nostoc are both heterocystic species. All these species are capable of both light and dark nitrogen fixation (Pearson et al 1981; Paerl 1990; Belnap, 1992). Since nitrogen fixation is an anaerobic process, species such as Microcoleus that lack heterocysts must utilize other methods. In oceanic systems, Microcoleus, as well as many other species, create anaerobic microzones through aggregation of filaments, both within and between sheaths (Pearlxxx).

Studies have shown that many types of disturbances negatively affects the cohesion and coverage of cyanobacterial-lichen crusts (Belnap and Gardner 1993; Cole 1991; Wilshire 1983). The most common disturbance to these crusts are compressional forces by livestock, human feet or off-road vehicles. Cyanobacterial filaments and lichens are brittle when dry and easily crushed by these compressional forces (Webb and Wilshire, 1983; Harper and Marble 1990; Belnap, 1993). These types of disturbance would have the potential of disrupting cyanobacterial aggregations. If anerobic microzone formation is dependent on filament and sheath aggregation for Microcoleus in soils, as it is in water (Paerl 1990), surface disturbances may reduce or eliminate the capability of these organisms to fix nitrogen.

Nitrogen fixation in these soil crusts has been examined on several occasions, with variable results. Nitrogen input estimates from these crusts has ranged from 4 to 365 kg/ha annually (Mayland et al. 1966; MacGregor and Johnson 1971; Rychert and Skujins 1974; Eskew and Ting 1978; Jeffries 1989). Nitrogen fixation in these crusts is highly dependent on past and present water and light regimes, as well as the species composition (Rychert et al. 1978). If these crusts depend on aggregation for fixation, determination of timing, extent and type of past disturbance may be a critical factor in determining fixation rates.

Response to, and recovery from, disturbance has been investigated in these crusts. However, response and recovery have traditionally been measured in terms of visual recovery, or biomass or numbers of organisms present in disturbed areas (Anderson et al 1982a, b; St. Clair et al 1986; Terry and Burns 1987; Brotherson et al 1983; Harper and Marble 1990; Belnap 1993; Cole 1991). What has not been addressed, however, is the effect of surface disturbance on the physiological functioning of these crusts. This study begins this process, looking at the effects of human trampling and off-road vehicles on nitrogenase activity of these cold-desert crusts.

MATERIALS AND METHODS

All sites were located with 10 miles of Moab, Utah, at an elevation of approximately 4500'. Three substrates were tested: soils derived from Navajo sandstone, Mancos shale and Paradox gypsum. On sandy soils, Coleogyne ramosissima (blackbrush) was the dominant vascular plant; on both the Mancos shale and gypsiferous soils, the vascular plant flora was dominated by Atriplex confertifolia. The areas chosen for study had well-developed cyanobacterial-lichen soil crusts. The cyanobacterium Microcoleus vaginatus was dominant in all the soils tested, often being the only cyanobacterial species present in any given sample. Sandy soil sites were in Arches National Park (north of Moab, Utah) and the Behind-the Rocks (BTR) area (south of Moab, Utah). At Arches, tracks were put in two types of crust. These were crusts that had only Microcoleus present (giving it a light appearance, and is referred to as "light" crust) and a second type with Microcoleus, some Scytonema myochrous and approximately 5% cover of the nitrogen-fixing soil lichen Collema tenax (giving it a dark appearance, and is referred to as "dark" crust). Treatments were

applied on 4/14/92, and sampled 4/14/92, 4/28/92, 6/2/92, 6/13/92, and 10/20/92. At the BTR site, crusts were similar to the dark crusts at Arches, again being dominated by Microcoleus, with some Scytonema and approximately 5% Collema present. Treatments were applied on 6/4/92, 9/30/92, 10/5/92, 10/19/92, 10/25/92, and 11/30/92. All were sampled the same day the treatment was applied. On the gypsiferous soils, Collema represented approximately 25%, with Microcoleus the only cyanobacterium consistently found. Treatments were applied 10/18/92 and sampled on 10/18/92 and 11/4/92. Mancos shale crusts were exclusively Microcoleus dominated, with no lichens present. Preliminary chlorophyll and nitrogenase assessments at the Mancos sites showed such low cyanobacterial biomass levels and low nitrogenase activity levels that this substrate type was dropped from further study.

Sandy and gypsiferous sites received selected treatments at 2 sandy and 3 gypsiferous sites. Treatments included 2 and 4 passes with a Toyota Landcruiser; 1 and 2 passes with a knobby-tire mountain bike; 1 and 3 passes with a knobbed, Vibram sole boot; 1 and 3 passes a smooth-soled sandal; and a small wooden block (15x30 cm) that was stepped on 1 time to compress the soil with the least churning action possible. Not all treatments were repeated at all sites. All soils were dry (gravimetrically determined) with the exception of gypsum sites 2 and 3, where soil moisture was 4%.

Nitrogenase activity and chlorophyll content were analyzed immediately after treatments were applied. Samples were collected dry. For nitrogen fixation, 20 samples were collected from each treatment. Samples were placed in clear, gas-tight tubes, the entire crustal surface was wetted equally with distilled water, and then injected with enough acetylene to create a 10% acetylene atmosphere. After injection, samples were incubated for 4 hours at 26 C in a chamber lighted with Chromo50 (5000 K) and cool white fluorescent bulbs. Subsamples (0.25 ml) of the head space within the tubes were then analyzed for acetylene and ethylene content on a Carle FID gas chromatography equipped with an 8 foot, 8% NaCl on alumina column, using helium as the carrier gas (30 ml/min).

For chlorophyll measurements, 15 samples per treatment were collected dry, and extracted immediately. The techniques outlined in Ronen and Galun (1984) were used. Chlorophyll was extracted from samples with dimethylsulfoxide (DMSO), in the dark for 45 minutes at 65 C. Samples were shaken, and a subsample then centrifuged. Absorption spectra were measured in a Hewlett-Packard diode array spectrophotometer, after calibration with a DMSO blank. Optical densities used for measurements were at OD 398 (chlorophyll a) and OD665 (both chlorophyll a and phaeophytin). Results were analyzed using analysis of variance (ANOVA), Duncan's multiple range test, and where only two treatments were applied, an unpaired t-test.

RESULTS

Results from these experiments are summarized in Table 1-4. As can be seen, almost all surface disturbances of any type significantly reduced nitrogenase activity in crusts at all sites. Cyanobacterial biomass, as measured by chlorophyll a levels, was

not significantly different from controls in any of the treatments. Since nitrogenase activity is highly dependent on past and current environmental variables, different sites or sample dates can only be compared with caution.

Wheeled Vehicles (Trucks and Mountain Bikes): All sites showed significantly lowered nitrogenase activity when driven across, with no significant difference between one or three passes. Vehicular tracks reduced nitrogenase activity in less well-developed (light) crust at Arches by 86-88%, and in dark crusts by 52-100%. At the BTR site, reductions were 40-92%. Mountain bike tracks were measured in the light crust at Arches, and reduced activity by 44-82%. At BTR, activity was decreased by 79%. Dark crusts showed less disruption of nitrogenase activity than light crusts when done on on the same day. For dark crusts on sandy soils where samples were repeated, early spring measurements (April) showed less disruption than summer and fall measurements (49-52% vs. 97-100%).

Gypsiferous soils showed a similar pattern, although activity differences were less. Three passes with a vehicle resulted in reductions of 48%. This site, resampled several weeks later, showed a reduction of 63%.

Footprints: Three types of shoes were used for footprints. These included boots and tennis shoes with lugged soles, and sandals with smooth soles. Experiments were done in dark crust only. Boots at Arches showed a 37-92% decline in activity. When compared with wheeled vehicle treatments on the same day, there were no significant differences. At BTR, the lugged boots and smooth sandals were compared: while the lug soles decreased activity by 79%, and was not significantly different from the wheeled vehicle treatment, smooth soles reduced activity by 50%. The smooth sole treatment was significantly less than the lugged sole or wheeled vehicles.

Gypsiferous soils showed a reduction of 60% when lugged boots were used. No disruption was seen with the smooth-soled sandals. Again, values for boots and vehicles were not significantly different from each other, but were significantly lower than smooth soles.

Wooden Block: This was used in sandy soils at the BTR site. This treatment resulted in a decrease of 25% in nitrogenase activity, the least disruption for any treatment on sandy soils.

DISCUSSION

Two known nitrogen-fixing species are dominant in the crusts used in these experiments. These include the filamentous cyanobacterium Microcoleus vaginatus (which constituted 75-95% of the ground surface) and the lichen Collema tenax (which made up 5-25% of the ground surface). Since nitrogen fixation is an anaerobic process, most cyanobacterial nitrogen fixation occurs in heterocysts, structurally differentiated, thick-walled cells that lack oxygen-evolving Photosystem II machinery. The phycobiont in C. tenax is Nostoc, a cyanobacterium with heterocysts, and Scytonema has heterocysts as well. However, M. vaginatus and M. chthonoplastes are non-heterocystic species, and thus must utilize

alternative ways of excluding oxygen in order to carry out fixation.

Nitrogenase activity has been demonstrated repeatedly in non-heterocystous aquatic species, including Aphanizomenon flos-aquae (Carlton and Paerl, 1989), Trichodesmium erythraea (Bryceson and Fay, 1981), Trichodesmium sp. (Paerl and Bebout 1988; Paerl et al., 1989b), Microcoleus chthonoplastes (Pearson et al., 1981), and Lyngbya aetuarii (Paerl et al., 1991). Separation of the nitrogenase enzyme from oxygen can be accomplished spatially, temporally or with a combination of both (Paerl, 1990). Trichodesmium, Microcoleus chthonoplastes and Aphanizomenon flos-aquae have been shown to create anerobic microzones spatially through aggregation both between and within sheaths. These species all showed reduced nitrogenase activity when shaken or when aggregates were disrupted (Paerl 1990). Many species also show continued, or increased fixation at night (Paerl, 1985; Paerl and Bebout, 1988; Carlton and Paerl, 1989, Paerl and Prufert, 1987; Bautista and Paerl, 1985). Bacteria associated with these species may be partially responsible for anerobic microzone formation through the scavenging of oxygen or may contribute N through their own fixation (Paerl et al., 1989a).

Since M. vaginatus fixes actively in light, with no significantly altered nitrogenase activity in the dark (Belnap 1992, unpublished data), this species must be capable of excluding oxygen spatially. Although all previous work done on microzone formation in non-heterocystic cyanobacteria has been with aquatic species, observations of soil crusts with a scanning electron microscope (Belnap and Gardner 1993) show that M. vaginatus could employ any or all of the strategies used by aquatic species: multiple trichomes within a single sheath may result in oxygen-free microzones (Bryceson and Fay 1891; Carpenter and Price 1976; Bautista and Paerl 1985; Paerl and Bland 1982), the packing of multiple sheaths on top of each other may result in an anaerobic environment within the sheaths located in the middle of this mat (Paerl and Prufert 1987), or associated bacteria may be scavenging oxygen (Paerl et al 1989a).

Results from this study support the hypothesis the aggregation is a major factor in the formation of microzones for M. vaginatus. Since there was no difference in chlorophyll levels among the treatments or the control, indirectly indicating that approximately the same number of cyanobacteria are present, the large differences seen in nitrogenase activity between treatments cannot be explained by differences in the number of nitrogen-fixing cyanobacteria present. If microzone formation was dependent only on bacterial scavenging, much less disruption of fixation would be expected from a single footprint than was seen in this study, and there little difference would be expected in fixation levels between the types of treatments used this experiment. Aggregations of cyanobacteria, however, would be disrupted by any surface disturbance. The more disruptive the disturbance, the more aggregates would be broken, and the greater reduction of nitrogenase activity would be expected. Lugged surfaces, such as tires on vehicles and mountain bikes, and Vibram soles on boots were more disruptive than smooth-soled sandals or wooden blocks on both sandy and gypsiferous soils

in this study. Lugged surfaces broke up and churned the soil. Smooth soles and wooden blocks tended to only compress the soil, thus better preserving the integrity of the soil surface. Greater amounts of compressional forces involved did not affect the results: bikes and Vibram soles were just as damaging as a vehicle. If aggregation amounts of compressional force would not be as important as the type of disturbance the surface received.

Similar results were obtained from another study done on fine-textured lacustrine soils at Dugway Proving Grounds in central Utah. Here, surface disturbances included shallow and deep raking; scalping of the top 1 cm of soil; and 1, 4 and 10 passes of a mobile howitzer (a tracked vehicle). All treatments showed a statistically significant 77-90% reduction in nitrogenase activity two years after the treatments were applied (Belnap et al, in review). Chlorophyll levels were not significantly different between controls and treatments that did not include scalping. Scalped plots still showed reduced chlorophyll levels after two years. However, there was no difference between nitrogenase activity in any of the treatments, regardless of the difference in chlorophyll levels. Again, the importance of packing would explain these observations: it is not just the number of cyanobacteria present, but their arrangement that is critical.

Relative to controls, dark crusts showed less disruption in nitrogenase activity than light crusts. This may be explained by the species present. Light crust is almost exclusively non-heterocystic Microcoleus sp., and therefore would be highly sensitive to any surface disturbance that would disrupt aggregations. Dark crusts contain heterocystic species such as Scytonema and Collema, making this crust somewhat less dependent on aggregation for nitrogenase activity.

Less reduction of nitrogenase activity was also seen on gypsiferous soils when compared to sandstone-derived soils. There are two possible explanations for this. First, dry gypsiferous soils are more cohesive, and have higher structural integrity, than dry sandy soils. Gypsum is highly soluble in water, and particles adhere to each other upon drying, instead of being loose like grains of sand. When stepped on, gypsiferous surfaces offer much more resistance than sandy substrates. Therefore, "packing" of the crust would more likely be preserved in a gypsiferous soil.

Secondly, there is more of the lichen Collema on gypsiferous crusts, occurring as scattered small dots throughout the crust. Since Collema has the heterocystous Nostoc as a phycobiont, it does not depend on other methods of excluding oxygen as do non-heterocystic cyanobacteria. As a result, disruption of packing would probably not result in a reduction of nitrogenase activity. However, since lichens are not mobile, greater reduction of nitrogenase activity could be expected over the long-term, as those pieces of lichen thalli buried by the disturbance would die, or disconnected pieces would be blown or washed away. In addition, cyanobacterial connections would be broken, and these particles subject to erosional forces as well. Both sites measured over time (vehicle tracks at Arches and gypsum) showed a decline in nitrogenase activity relative to controls.

This study has many implications for ecosystems which are dependent on these crusts for nitrogen. Since many of the cold-desert systems in which these crusts occur have few, if any, nitrogen-fixing plants, surface disturbances (such as trampling by livestock, people and/or recreational vehicles) could result in dramatic decreases in nitrogen input from these crusts and would consequently have ecosystem-wide effects. Results from a study done by Belnap and Harper (1993, in review) show that plants growing in uncrusted areas have significantly lower nitrogen content than plants growing in well-developed crusts. Evans and Ehrlinger (1993) showed that crusts were the predominant source of nitrogen for the two juniper woodland sites measured. In addition, preliminary work done using stable isotopes of nitrogen indicate that plants growing in areas with well-developed crusts have more, and more recently "fixed", nitrogen in their tissues than plants in neighboring areas with a more disturbed crust (Evans and Belnap unpublished data). Since these cold-deserts have been grazed extensively for 100 years, and now are receiving ever-increasing recreational uses, understanding of the relationship between surface disturbances and nitrogen cycles is critical.

This study also forces a re-examination of the definition of recovery for these soil crusts. Traditionally, recovery has been defined visually, or by using estimations of biomass. Estimates of recovery from trampling with these techniques vary from a few to 100 years (Belnap, 1993; Anderson, et al, 1982a; Anderson et al 1982b; Brotherson, et al 1983; Cole, 1991; Ashley and Rushforth, 1984; Johansen and Rushforth, 1985). However, it is clear that the physiological functioning of these crusts needs to be included in these estimates. Indications from this study and the study at Dugway point to a slow recovery for nitrogenase activity: no recovery was seen after 9 months at Arches and BTR, and no recovery was observed at Dugway after 2 years. Since these microbial organisms are only metabolically active when wet, and rainfall is sparse, recovery could take many years.

There is a great deal that is unknown about the effects of surface disturbance on these crusts. Only one aspect of their physiology, nitrogenase activity, has been examined relative to disturbance. There may be other physiological aspects that are disrupted as well. Until such time that further studies can be done, and recovery time from such disturbance can be better estimated, it is important that these resources be managed conservatively.

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Table 1. Arches site: Percent decline of nitrogenase activity with different surface disturbances at 7 sampling dates. All declines were significantly different from controls.

Table 2. Behind-the Rocks (BTR) site: Percent decline of nitrogenase activity with different surface disturbances at 7 sampling dates. All declines were significantly different from controls except sandal and wood.

Table 3. Gypsum site: Percent decline of nitrogenase activity with different surface disturbances at 2 sampling dates. Vehicles and boot treatments were significantly different from the control; sandal treatment was not.

DATE	VEHICLE 3 PASSES	BOOT 1 PASS	SANDAL 1 PASS
10/18/92	48%	60%	0%
11/4/92	63%		

DATE	CRUST TYPE	VEHICLE 1 PASS	VEHICLE 3 PASSES	BIKE 1 PASS	BIKE 3 PASSES	BOOT 1 PASS	BOOT 3 PASSES
4/14/92	L	88%					
	D	52%					
4/16/92	D		66%				
	L			63%			
	L				82%		
	L			44%			
	L				63%		
4/18/92	D					60%	
	D						92%
4/28/92	D					42%	32%
	D					48%	37%
	L	86%					
	L		85%				
	D	49%					
6/2/92	D	98%					
	D		95%				
6/13/92	D	97%	100%				
10/20/92	D	100%					
	D	100%					

DATE	VEHICLE 1 PASS	BIKE 1 PASS	BOOT 1 PASS	TENNIE 1 PASS	SANDAL 1 PASS	WOOD DRY
6/4/92	69%					
6/6/92		79%	79%		50%	
6/7/92			62%		38%	25%
9/30/92			61%	81%		
10/5/92	92%		85%	96%		
10/19/92			50%	85%		
10/25/92	91%					

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SURFACE DISTURBANCE OF CRYPTOBIOTIC SOIL CRUSTS: EFFECTS ON
NITROGENASE ACTIVITY, CHLOROPHYLL CONTENT AND CHLOROPHYLL
DEGRADATION

ABSTRACT

Cryptobiotic soil crusts are an important component of semi-arid and arid ecosystems. One of their more important roles is the contribution of fixed nitrogen and carbon to these systems. This study examined the effects of different surface disturbances (raking, scalping, and tracked vehicles) on nitrogenase activity, chlorophyll content and chlorophyll degradation in these crusts two years after the disturbances. Any disturbance was found to reduce nitrogenase activity by 77-97%, with no significant recovery seen after the two years. Chlorophyll content was significantly lower in the scalped treatments, and not different between any of the others. Therefor, recovery of this characteristic is fairly quick unless surface material is removed. No differences were seen in chlorophyll degradation rates between the treatments. Reasons for rapid recovery of chlorophyll, and non-recovery of nitrogenase activity is discussed.

INTRODUCTION

Cyanobacterial-lichen soil crusts are extremely common throughout the semi-arid and arid landscapes of the world, representing up to 70% of the living cover in some of these systems. These crusts contribute in many ways to the ecosystems in which they occur. Contributions include enhancement of soil stability by reducing both wind and water erosion, by the production of microcatchments on soil surfaces, the absorptive properties of cyanobacterial sheath material, and the ability of this sticky sheath material to bind soil particles together and thus prevent their movement (Belnap and Gardner 1993; Fletcher and Martin 1948; Kleiner and Harper 1972, 1977; Loope and Gifford 1972; Anderson et al., 1982a, 1982b; Harper and Marble 1990; Shields and Durrell 1964; Anantani and Marathe 1974; Anderson and Rushforth 1976; Campbell 1979; Maranthe 1972; Metting and Rayburn 1983).

Crusts can increase the nutrient status of soils. Cyanobacteria and cyanobacterial components of soil lichens fix atmospheric nitrogen (Belnap 1992; Skujins and Klubek 1978; West and Skujins 1977; Terry and Burns 1987; Fuller et al., 1960). Studies utilizing radioactive isotopes of nitrogen have demonstrated that nitrogen fixed by cyanobacteria in the crusts is available to, and used by, neighboring vascular plants (Mayland et al., 1966; Mayland and McIntosh 1966). In some desert systems, these crusts have been demonstrated to be a dominant source of this often-limiting element for associated seed plants (Evans and Ehrlinger, unpublished data). Plants growing in these crusts show

elevated levels of most soil macronutrients when compared to plants in uncrusted soils (Harper and Belnap, 1993).

The presence of soil crusts can also affect seedling establishment and survival. Experiments done by K. Harper (unpublished data) in sites with both fine and coarsely-textured soils demonstrate that seedling establishment was much higher in crusted areas when compared to areas where the crust had been removed for both forbs and grasses. Survival over a three year period was enhanced in the four species (grasses and forbs) measured at these sites as well. Other studies have reported similar enhancement of seedling germination and establishment in crusted areas when compared to non-crusted surfaces (Harper and St. Clair 1985; St. Clair et al., 1984).

Trampling negatively affects the cohesion and coverage of cyanobacterial crusts, since the filaments are brittle when dry and both the cyanobacteria and lichens are easily crushed (Harper and Marble 1990; Belnap, 1993). Recovery from disturbance has been studied by several investigators. Recovery has been defined in terms of either biomass of cyanobacteria and green algal, or the recovery of visual aspects of the crust. Based on this, recovery rates have been found to depend on the type and extent of disturbance, the availability of nearby inoculation material, as well as on the temperature and moisture regimes that follow disturbance events. Estimates of time for unaided recovery of cryptobiotic crusts from disturbance have varied widely, ranging from a few years to 100 years for full recovery of all components (Anderson et al., 1982b; Jeffries and Klopatek 1987; Callison et

al., 1985; Cole 1991). Belnap (1993) estimates that crusts on sandy soils on the Colorado Plateau require at least 40 years for recovery under stable soil conditions.

There is, however, another aspect to disturbance and recovery that has been neglected. This aspect addresses the physiological functioning of these crusts. This study begins the examination of this aspect of recovery by looking at the effects of different disturbance on nitrogenase activity, chlorophyll degradation and chlorophyll content of these crusts, and recovery from these disturbances.

MATERIALS AND METHODS

Plots were located at Dugway Proving Grounds, Utah. This area is a fine-textured, lacustrine silt/clay dominated by Kochia americana and Atriplex confertifolia. The area chosen for study had a well developed cyanobacterial-lichen soil crust, with lichens and cyanobacteria representing, on the average, 24% and 47% of the ground cover respectively. Of the lichens present, only Collema sp. is known to fix nitrogen; it represented ---% of the ground cover. Of the cyanobacteria present, Microcoleus vaginatus was dominant, often being the only cyanobacterial species present in any given sample. This area had not been trampled by livestock, vehicles or foot traffic for over --- years. Treatments were applied in ---, 19---. Randomized blocks were used, with 3 blocks and --- treatments. Treatments included shallow raking (top --cm); deep raking (top --cm); scalping of the top --cm of soil; driving over with a tracked vehicle (mobile howitzer) 1, 4, and 10 times;

and scalping plus driving over 4 times. These treatments were applied to dry soils.

Nitrogenase activity and chlorophyll content were analyzed in April, 1992, approximately ---months after the plots were established. Samples were collected dry. For nitrogen fixation, 20 samples were collected from each treatment. Samples were placed in clear, gas-tight tubes, the entire crustal surface was wetted equally with distilled water, and then injected with enough acetylene to create a 10% acetylene atmosphere. After injection, the crusts were incubated for 4 hours at 26 C in a chamber lighted with Chromo50 (5000 K) and cool white fluorescent bulbs. Subsamples (0.25 ml) of the head space within the tubes were analyzed for acetylene and ethylene content on a Carle FID gas chromatography equipped with an 8 foot, 8% NaCl on alumina column, using helium as carrier gas (30 ml/min).

For chlorophyll measurements, 15 samples per treatment were collected dry, and extracted immediately. The techniques outlined in Ronen and Galun (1984) were used. Chlorophyll was extracted from samples with dimethylsulfoxide (DMSO), in the dark for 45 minutes at 65 C. Samples were then centrifuged. Absorption spectra were measured in a Hewlett-Packard diode array spectrophotometer, after calibration with a DMSO blank. Optical densities used for measurements were determined by scanning between 700 and 400 nm both non-acidified and acidified (using 1N HCl) extracts. Acidified extracts of the cyanobacterial soil crusts showed a drop at OD398 (chlorophyll a), and a new peak at OD362 (phaeophytin), and a drop at OD665 (both chlorophyll a and

phaeophytin). Consequently, measurements were made at 362nm and 398 nm for chlorophyll degradation ratios, and at 665nm (chlorophyll a) before and after acidification (with 1N Hcl), and 750 (turbidity) for chlorophyll a per unit surface area. Chlorophyll a was determined using an equation modified to express pigment content on the basis of surface area:

$$\mu \text{ chl } \underline{a} \text{ cm}^{-2} = \frac{26.73 (*) (v)}{(A) (L)}$$

where (*) is the difference in absorbance before and after acidification (of 665nm -750nm); (v) is the extract volume in ml; (A) is the surface area of the sample in cm²; and (L) is the path length of the spectrophotometer cuvette in cm. This equation accounts for any phaeophytin or turbidity in the sample (Beymer and Klopatek, 1992). Chlorophyll degradation ratios were constructed using 398nm/362nm. Results were analyzed using analysis of variance (ANOVA) and Duncan's multiple range test.

RESULTS

Results for nitrogenase activity, ranked according to activity levels, are shown in Table 1. The control (T1) shows significantly higher nitrogenase activity levels (35.5 picomoles/hr.) than the other treatments (ranging from 1.0 to 8.0 picomoles/hr). This represents a 77-97% reduction in nitrogenase activity, with a mean

reduction of 88%. The treatments were not significantly different from each other.

Chlorophyll content was only significantly different between the two scalped areas and the shallow raked and one-pass treatments. As would be expected, the scalped treatments were lower than the rest of the plots. The rest of the treatments were not significantly different from each other. Chlorophyll degradation showed no significant effects between treatments (Table 2).

DISCUSSION

Clearly, all of the disturbance treatments greatly reduced nitrogenase activity in the crusts. Even though this study was done ---months after the initial disturbance, little, if any, recovery of nitrogenase activity has taken place.

Several nitrogen-fixing species were present in these crusts before disturbance. The lichen Collema sp. is known to be an active fixer (Belnap, 1992). However, this lichen is very sensitive to both trampling and burial by sediments. When dry, it is brittle and easily broken by compressional forces, and many of the small pieces are often blown away or buried by the trampling action. Even if pieces are left on the surface, nearby disturbances often create enough wind- or water- borne sediments to bury some. Since this lichen generally cannot grow quickly enough to reach the surface before exhausting its resources, burial often means death. Consequently, most disturbances would result in a

reduction of this lichens' contributions to nitrogen-fixing activity and chlorophyll content in the plots.

Soil cyanobacteria are also capable of nitrogen fixation. Although there were several known fixers identified from this crust in this area, the only species with a significant amount of biomass was the cyanobacterium Microcoleus vaginatus. This cyanobacterium has multiple filaments contained within an extracellular sheath (Fig. 1). It is a non-heterocystous species, but is known to fix nitrogen in soils throughout the Colorado Plateau (Belnap, 1992). It is not known how the oxygen exclusion necessary for nitrogen fixation is accomplished in this species without the presence of heterocysts. It is possible that an anaerobic environment is obtained either within the sheath itself, or more likely, that groups of sheaths packed together are able to exclude oxygen. This packing could be accomplished with sheaths with or without living filaments inside. If this is true, then virtually any disruption to this packing could create an oxygenated environment, thereby stopping nitrogen fixation. Since the structure of these crusts is extremely fragile, especially when they are dry and the sheath material is brittle, virtually any surface disturbances would result in a cessation of nitrogen fixation.

Most cyanobacteria are much more tolerant of burial than soil lichens. M. vaginatus can move readily through soils when they are wetted, often traveling up to 5 cm in 24 hours (S. Campbell, personal communication). This enables them to generally reach photic zones even though covered by water- or wind- borne sediments. For this reason, it is not surprising that one-time

surface disturbances that did not actually remove material would not result in significantly different chlorophyll levels. Scalped plots, where material was removed, would be expected to have lower chlorophyll contents until enough time had passed for these microbial populations to re-establish themselves. Since these organisms are only active when wet, recovery time for chlorophyll contents would be heavily rain-fall dependent.

Recovery of nitrogenase activity in M. vaginatus-dominated systems, however, could take much longer. Since the amount of chlorophyll present is not significantly higher in the control plot when compared to any of the treatments, yet nitrogenase activity is, nitrogenase activity is clearly not solely determined by the number of cyanobacterial cells present. If nitrogenase activity is dependent in some way on packing of this cyanobacterium, then recovery of activity would be more closely related to the production of sheath material and/or filaments. Nothing is really known about rates of production for either of these components. Sheath material is produced whenever this cyanobacterium is wetted and its filaments extruded (Belnap, personal observation), but there is no information on rates, or what controls them. Nothing is known about what controls the production of filaments, or what determines the number of filaments per sheath. It has been noted that the number of filaments per sheath tends to be higher in gypsiferous and limestone soils, as well as sandy soils that have not been subjected to trampling by livestock or humans (Belnap, 1992).

This study raises many questions critical to the effective management of semi-arid landscapes. These systems are already notoriously low in nitrogen, and activities that affect input of this often-limiting nutrient need to be taken seriously. Research is needed to understand the mechanisms controlling nitrogenase activity in these crusts, and ways that disturbance affects this activity. With this information, management actions can then be developed that will allow us to both minimize damage to these systems and hasten their recovery.

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TABLE 1. Nitrogenase activity measured for the different treatments. The control treatment was significantly different from all other treatments at the $p < 0.02$ level. (Different letters denote statistical difference).

TREATMENT	NITROGENASE	
	ACTIVITY	
	Picomoles/hr	p
Control	35.5	a
Deep raked	8.0	b
One pass	5.3	b
Shallow raked	4.0	b
Ten passes	3.8	b
Scalped, four passes	2.9	b
Four passes	2.3	b
Scalped	1.0	b

TABLE 2. Chlorophyll content and chlorophyll degradation ratios measured in the different treatments. Different letters denote statistical differences at the $p < 0.05$ level. No significant differences were found in chlorophyll degradation ratios.

TREATMENT	CHLOROPHYLL	CHLOROPHYLL
	CONTENT	DEGRADATION

	$\mu\text{g}/\text{cm}^2$	p	OD362/OD398
One pass	5.3	a	.94
Shallow raked	4.8	a	.95
Control	4.2		.98
Ten passes	3.9		.95
Deep raked	2.6		.91
Four passes	1.1	b	.96
Scalped	1.0	b	.99
Scalped, four passes	1.0	b	.96

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Work Plan:

We plan to delineate 18 plots (3X9m) in an area 40X40m near the SERL site in Dugway Proving Grounds. In each plot, six permanent meter square quadrats will be established. Two of these quadrats will be burned, two will be trampled, and two will serve as controls (no disturbance). Treatments will be assigned randomly.

Burning of the designated quadrats will be accomplished by placing a steel barrel (1m diameter) over the quadrat and introducing propane flame jets from holes near the bottom of the drum for 20 seconds. This produces an evenly burned surface without risk of starting rangefires. Burning will take place in the fall as soon as permission to procede is received (likely the last week in September).

Trampling will be conducted by walking repeatedly on the designated quadrats. Trampling will be conducted several times in the fall. The first trampling will be done when plots are burned. The second trampling will take place the week of October 26-30. A third trampling will take place the first week in December (Nov. 30-Dec. 4).

Cover of vascular plants and cryptogams will be measured using nondestructive techniques (quadrats and point methods). Very small (1 cm³) soil samples will be taken for estimating algal biomass. At the beginning of the study, the soils will be characterized by removing 100 cm³ of soil from each plots for soil analysis. Cyanobacteria will be isolated from the soil and methods of mass culture of these organisms will be studied through the fall and winter of 1992.

Cyanobacterial ammendments will be applied to half of the quadrats between April 8-12, 1993. We will likely apply Microcoleus vaginatus, Nostoc commune, and Tolypothrix bristoliana, species which we know occur at the Dugway site. We will then monitor the establishment of these algae in the inoculated quadrats. We will visit the site to collect soil samples the weeks of May 17-21, 1993 and August 23-27, 1993.

Some of the plots will be tested for sedimentation following the first treatments (trampling, burning) in the fall of 1992. They will be tested again the week of August 23-27, 1993, and again 1 year later. This procedure entails placing a rain machine over the quadrats, raining 5 gallons of water on the quadrat, and

collecting the runoff with sediment from the quadrat.

Although our funding will likely cover only a two year time period, we are interested in following the long term recovery of the cryptogamic crusts, and so would like to continue to visit the site as time permits over the next five years. On these follow-up visits, only small (1 cm^3) soil samples will be removed. Cryptogamic cover will also be estimated using quadrats.

1 ☒ ☐ T	10 ☐ ☒ T	19 ☐ ☒ T	28 ☐ ☒ C	37 ☐ ☒ T	46 ☒ ☐ C
2 ☒ ☐ F	11 ☒ ☐ F	20 ☐ ☒ F	29 ☐ ☒ T	38 ☒ ☐ F	47 ☒ ☐ T
3 ☐ ☒ C S	12 ☒ ☐ C S	21 ☐ ☒ C S	30 ☐ ☒ F S	39 ☒ ☐ C E	48 ☒ ☐ F E
4 ☒ ☐ T	13 ☐ ☒ C	22 ☒ ☐ T	31 ☒ ☐ F	40 ☒ ☐ T	49 ☐ ☒ C
5 ☒ ☐ F	14 ☐ ☒ T	23 ☒ ☐ C	32 ☒ ☐ C	41 ☐ ☒ F	50 ☐ ☒ T
6 ☒ ☐ C E	15 ☒ ☐ F S	24 ☐ ☒ F E	33 ☐ ☒ T S	42 ☒ ☐ C S	51 ☒ ☐ F E
7 ☒ ☐ C	16 ☐ ☒ F	25 ☐ ☒ C	34 ☒ ☐ C	43 ☐ ☒ C	52 ☒ ☐ T
8 ☐ ☒ T	17 ☐ ☒ C	26 ☐ ☒ F	35 ☐ ☒ T	44 ☒ ☐ F	53 ☒ ☐ F
9 ☒ ☐ F E	18 ☒ ☐ T E	27 ☒ ☐ T S	36 ☐ ☒ F E	45 ☐ ☒ T E	54 ☒ ☐ C S

T = Trample

F = Fire

C = Control

S = sedimenta

E = eumetazoa

I = plot to be

Table 4. Relative Colonization of roots by Rhizosymbionts on Cyanobacterial Crusted vs. Comparable soils without a Biotic Crust

<u>Species*</u>	<u>Associate Microbe</u>	Average Percent of Root Length Colonized (N = 5 in each Group)	
		<u>No Biotic Crust</u>	<u>Cyanobacterial Crust</u>
<u>Bromus tectorum</u>	VA Mycor.	3	8
<u>Coleogyne ramosissima</u>	VA Mycor.	5	18
<u>Festuca octoflora</u>	VA Mycor.		
Colorado Plateau		T	1
Washington County		2	4
<u>Lupinus pusillus</u>	Rhizobia	22	34
<u>Plantago patagonica</u>	VA Mycor.	No Sample	13
<u>Stipa hymenoides</u>	Rhizosheaths	40 weak	100 (60% strong)

* Roots of the following species were studied, but no mycorrhizae were observed: Cryptantha pterocarya, Cryptantha crassisejala, Mentzelia albicaulis, and Streptanthella longirostris. All of these species are annuals.

